Review of the Effects of Enhancement Strategies on Interactions among Juvenile Salmonids

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by

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ABSTRACT

The literature and available information on interactions between juveniles of cultured and wild stocks of Pacific salmon and anadromous trout was reviewed. The objective was to document the existing information and to identify and assess areas of concern in the planning and implementation of enhancement facilities. Information was gathered through a search of the published literature as well as less formal sources including the personal observations of enhancement workers. It was noted that all juvenile salmonids interact with other species to some extent and that the most extensive and best documented interactions appeared to occur in those species that spent one or more years in fresh water. These species typically interact competitively with other species in their first year and as potential predators in later years. Interactions are usually size mediated and as all species of salmon and trout are to some extent piscivorous, enhancement manipulations which result in high mixed stock concentrations usually result in displacement or mortalities in the subdominant group. It was concluded that enhancement programs should incorporate a number of basic studies in the planning process in order to determine the potential for detrimental interactions and to mitigate against these effects.

RÉSUMÉ

Nous avons passé en revue la documentation et les renseignements accesibles sur les interactions des juveniles de stocks cultivés et naturels de saumons du Pacifique et de truites anadromes. Notre objectif était de documenter les informations recueillies et de cerner les problèmes possibles dans la planification et l'établissement d'installations de mise en valeur des espèces. Pour faire notre synthèse, nous nous sommes appuyés tant sur la documentation publiée que sur des sources moins officielles, comme les observations personnelles des techniciens de la mise en valeur des stocks de poissons. Nous avons noté que tous les salmonides juvéniles ont certaines réactions avec d'autres espèces et que les interactions les plus importantes et les mieux documentées se produisent chez les espèces qui passent une ou plusieurs années en eau douce. Ces espèces sont typiquement en compétition avec les autres au cours de leur première année et deviennent des prédatrices potentielles au cours des années suivantes. Les interactions sont généralement fonction de la taille des poissons et comme toutes les espèces de saumons et de truites sont piscivores, jusqu'à un certain point, les manipulations en vue de l'amélioration des espèces, qui provoquent de fortes concentrations de stocks mixtes, entraînent généralement le déplacement et la mortalité du groupe sous-dominant. Nous avons conclu de notre analyse que les programmes de mise en valeur des stocks devraient inclure un certain nombre d'études de base, à l'étape de la planification, afin de définir les interactions nocives éventuelles et d'en réduire les effets.

INTRODUCTION

OBJECTIVES

This project was commissioned by the Department of Fisheries and Oceans (DFO) through the Department of Supply and Services (DSS file no. O4SB.FP576-3-2461). The objective was to identify and assess areas of concern to the planning and development of enhancement strategies that might involve interactions among juvenile salmonids and other fish. The study reviews and documents existing knowledge concerning competition and predation among enhanced stocks, and between enhanced and wild stocks, of juvenile salmonids.

BACKGROUND

Biological interactions are many and not always easily defined. In the salmonid enhancement context the term generally means some form of ecological interaction such as competition or predation. Thus, the concern about interactions evolves primarily from the potential for enhanced stocks to influence growth, survival and numbers of wild stocks or other enhanced species. Because the target species of enhancement projects live in real worlds, they interact with competitors and predators, and some of these competitors and predators are other juvenile salmonids. Indeed, evidence is accumulating in the general ecological literature (see Schoener, 1983 for a review) supporting the intuitive view that closely related species probably interact more strongly than distantly related species and that intraspecific interactions (e.g. competition among stocks of the same species) are likely to be more severe than interspecific interactions. Thus, concern about negative interactions among juvenile salmonids produced by different enhancement projects, is legitimate.

The present review examines the literature on interactions among juvenile salmonids and attempts to determine if such interactions are of actual, or potential, importance to salmonid enhancement activities. Before proceeding to the results of the study, however, the two major classes of interactions (competition and predation) are reviewed and some problems involved in evaluating their potential importance for juvenile salmonids are discussed.

Competition

Most ecologists think of competitive interactions as one of the primary forces involved in microevolution and the structuring of animal communities. As a result, much research has attempted to evaluate the importance of competitive interactions in nature. These efforts have met with only limited success. The reasons for this are reviewed by Schoener (1983), but part of the problem is that there are several classes of competitive interaction (e.g. exploitive and interference competition) and that these interactions can be direct or diffuse. In addition, there are many resources for which animals can compete. Unfortunately, resources are seldom stable and usually their availability varies through time. Hence competitive interactions may be ephemeral and only demonstrably important when there is a so-called "resource crunch" (Weins, 1977). Attempts to investigate the role of competition in nature often founder on the complexity of biological systems and it is rare to find a study that unequivocally demonstrates the importance of competition.

Despite these problems, however, there is a large body of observational data consistent with the view that competitive interactions are important regulators of animal numbers and survival. In fishes, these observations suggest that interspecific competitive interactions are often exploitive and diffuse. That is, fish species compete by exploiting the same resources (food and space seem particularly critical (Keast, 1978)) and this competition often involves a number of interacting species. Typically, such observations involve documenting a species' biological characteristics (use of food and space, growth rate, ultimate size, etc.) where it occurs without a competing species (allopatry) and where the two species occur together (sympatry). Differences in such characteristics between allopatric and sympatric populations can then attributed to competitive interactions. A good example of this type of analysis is the study of interactions between rainbow and cutthroat trout in coastal British Columbia lakes (Nilsson and Northcote, 1981). Obviously, such studies should involve a number of populations in each category, but if there are consistent differences in the biological characteristics of the two species when they are allopatric and sympatric, then the inference that competitive interactions are important seems reasonable.

With the exception of introductions (transplants) and territorial species, interference competition seems to be less common than exploitive competition in fishes. Nilsson (1967, 1978) has stressed the importance of interactive segregation in salmonid fishes. He distinguishes between interactive and selective segregation and argues that interactive segregation results from direct interactions between species (i.e., aggression, food scrambling, etc.) whereas selective segregation results from species being adapted to different life styles. Nilsson's interactive segregation appears to be some form of interference competition. Most of his examples involve niche shifts that occurred after the introduction of one species into a lake containing another related species. Changes in the use of food and space that occur immediately after such an introduction probably are attributable to interference effects; however, as Miller (1954) demonstrated, one generation in a new environment is sufficient to produce detectable changes in a salmonid stock. If such changes have a genetic basis, then Nilsson's distinction between interactive and selective segregation can become blurred within the first generation after an introduction.

In territorial species interference competition can be extremely important. In an elegant field experiment, Miller (1958) demonstrated that interference competition between resident cutthroat trout and a hatchery stock of the same species resulted in a 30 to 60 percent mortality in the hatchery stock within two weeks after release. Similar effects might be expected in juvenile coho, particularly in stocks (such as interior fish) released at relatively long distances from the sea. Certainly there are differences in the inherited levels of aggression between coho stocks (Roseneau, 1984) and thus the potential for interference interactions clearly exists.

Although most of the evidence for the importance of competitive interactions between juvenile salmonids is of the observational - deductive type, there is also some "hard" evidence. This hard evidence comes from field experiments. Typically, some aspect of a putative competive interaction is manipulated and any changes in ecological niche breadth, survival, or growth are recorded. Unfortunately, field experiments are difficult to control tightly. Thus the results are often open to interpretation. Despite this limitation, field experiments provide the best available data on competitive effects. An example is the study of brown trout - brook trout interactions in Michigan streams (Fausch and White, 1981). This study clearly demonstrates the importance of competition for space between these species, but equally clearly demonstrates the difficulties in interpreting the results of field experiments. In choosing case histories for inclusion in this review we have tried to emphasize examples that involve some form of manipulation. The reason for this procedure is that field experiments generally provide more rigorous data than simple observation.

Predation

Like competitive interactions, predator - prey relationships in fishes are often complex and characteristically change with size. Thus, as Larkin (1979) indicates, many species that are prey at one stage in their life history become predators at some later stage. This is particularly true in salmonids. For example, coho fry are often subject to trout and Charr predation but by the time they reach smolt size they can become major predators on chum and pink salmon fry (Pritchard, 1936). Predator - prey interactions can also be inextricably entangled with competitive interactions (Fausch and White, 1981) so that predator induced changes in prey density may feed back into, and strongly influence, competitive interactions among species.

Investigations of the food habits of fishes (especially salmonids) are numerous and one of the few clear generalizations that emerges from all of this information is that it is rare for any species to eat only one class of prey (Larkin, 1956). This does not mean that fish do not show strong prey preferences - they clearly do. These preferences, however, are not fixed and prey switching is a common aspect of fish foraging behaviour (Hyatt, 1978). In general, if a particular prey increases in abundance, fishes will switch to that prey; however, they rarely consume a prey species in direct proportion to its abundance in the environment. Usually, some form of frequency dependent selection appears to operate in fishes (Popham, 1942). Thus, rare prey are eaten less frequently than expected from their abundance in the environment; whereas abundant prey are taken at a higher frequency than expected from their abundance (Clarke, 1962). The behavioural and perceptual mechanisms that produce this effect are not well understood, but theirimportance to juvenile salmonid predatory interactions is clear. This phenomenan allows many predators (including other salmonids) to capitalize on temporary concentrations of prey such as fry and downstream migrants.

The effects of predation on prey abundance are usually considered under three categories: depensatory, compensatory and extrapensatory effects (Neave, 1953). The two that are of concern here are depensatory and compensatory effects. They are linked to prey density, whereas extrapensatory effects are independent of prey density. Depensatory mortality occurs when the proportion of prey consumed is inversely related to prey density; compensatory mortality occurs when the proportion of prey consumed is directly related to prey density. For juvenile salmonids migrating downstream or passing through an estuary or some other restricted area, initial mortality due to predators is probably compensatory. That is, as prey density rises the predators begin to switch to this increasingly abundant prey and the proportion of prey taken rises. However, unless the predators can increase their numbers rapidly (presumably by migrating from surrounding areas) they soon become saturated and the mortality becomes depensatory. Thus, fry moving en masse are likely to suffer smaller proportional losses than small aggregations.

Changes in the response of predators as prey density changes are also an important component of predator - prey interactions (Solomon, 1949: Holling, 1959a). Such responses fall into two general catagories: 1) functional responses, and 2) numerical responses. Functional responses involve changes in the number of prey eaten per predator per unit of time; whereas numerical responses involve changes in the number of predators as prey density changes.

Functional responses can be complex and several different types have been described (Holling, 1959b; Peterman and Gatto, 1978). The functional responses that appear to be potentially important in salmonid predator - prey interactions are types II, III and IV (Figure 1).

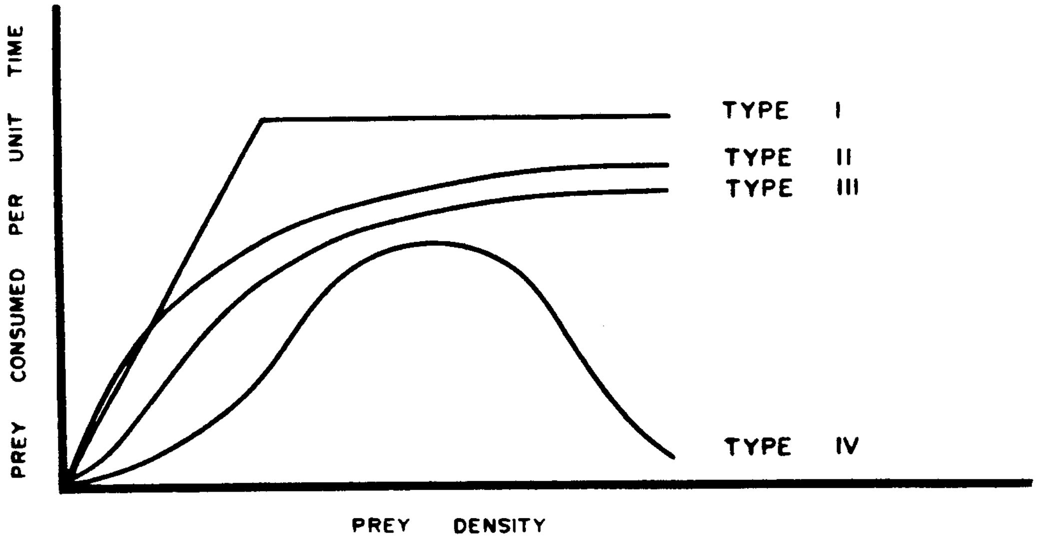

Figure 1. Predatory Functional Responses (after Peterman and Gatto, 1978: Woodsworth, 1982).

In a Type II functional response "handling time" limits the rate of predation. Thus as prey density increases the rate of the number of prey eaten per unit of time decelerates and eventually reaches an asymptote. In contrast, the type III response curve is sigmoid. The acceleration phase of this curve results from either the predator learning to handle or attack the prey more efficiently (Hollings, 1966: Begon and Mortimer, 1981) or from prey switching (Oaten and Murdoch, 1975). Ultimately, however, this curve also decelerates and reaches an asymptote. Prey-switching can also effect the type II response (Peterman, 1977) particularly if the switch to a specific prey is sudden. In salmonid predator - prey relationships, it is often difficult to distinguish between type II and type III responses (Woodsworth, 1982). The type IV response also involves an increase in predation, but at high prey densities the rate of predation decreases. This decrease in predation rate with increased prey density is usually explained by mechanisms such as prey schooling and the resultant confusion effects when a predator attacks into a school (Partridge, 1982).

Numerical responses by predators can occur over short or long time scales. Short-term responses involve predators aggregating in areas of increased prey density. Such responses clearly are important relative to release strategies. Long term numerical responses involve changes in the population size of predators. Again, there is a potential for impact on enhancement projects, although it is not clear that such changes would be important. For example, a successful lake enrichment program might, over a period of years, result in increased populations of trout and charr and thus increase predation on sockeye fry.

As was the case for competitive interactions, there is a large body of observational data that suggests that predatory interactions are an important determinant of salmonid population densities. Since the smolts of some species prey on the fry of other species it is reasonable to infer that under the right conditions predator - prey interactions could seriously affect the productivity of some salmonid enhancement projects. There is now enough known about migration times, size differences between species, and feeding and digestion rates to model the potential impact of one species on another. Such exercizes (Belford, 1978; Woodsworth, 1982; Mace, 1983) suggest that predation may be important. However, like the data on competitive interactions, there is much inference but little evidence. Again, the best evidence concerning the importance of predation by juvenile salmonids on other salmonid species comes from field experiments. The case of Stilliguamish pink salmon (Aimes, in prep.) and their interaction with an enhanced coho stock is one of the few direct, manipulative examples of a significant predatory interaction between juvenile salmonids.

METHODS

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

LITERATURE SEARCH

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

Computer Search

The computer search was performed by the Woodward Biomedical Library at the University of British Columbia. Data bases searched included:

Aquaculture	1970 - 1983
Candle	1972 - 1983
NTIS	1964 - 1983
ASFA	1978 - 1983

The following key words were used:

- salmon
- trout
- juvenile
- fry
- parr
- smolt
- hatcheries
- fish culture
- enhancement
- predation
- competition
- segregation
- co existing
- sympatric
- interrelationship
- displacement

Manual Search

In addition to the computer search, the Canadian Journal of Fisheries and Aquatic Sciences (1960-1983) and the Transactions of the American Fisheries Society (1960-1983) were searched. In addition, various technical publications associated with these journals were also searched.

Letters of Enquiry

To increase the breadth of the search, letters of were sent to institutions engaged in salmonid research. The institutions canvassed are summarised below:

INSTITUTIONS	NUMBER
- provincial fish and wildlife agencies	4
- state fish and wildlife agencies	25
- DFO offices in Quebec and the Maritimes	5
- universities in the United States	12
- government and university research centres in Japan	3
- universities in Norway	1
- fisheries research laboratories in the United Kingdom	3
- state enhancement agencies, cooperative fisheries research units and aquaculture cooperatives or corporations in Alaska, Washington, Oregon, California and Idaho.	22
Total	75

INTERVIEW PROGRAM

At the outset of the program it was assumed that published literature would be sparse, and that the bulk of information would come from either the 'grey literature' contained in agency and university technical reports or the unpublished observations of people directly involved in either salmonid enhancement or the study of juvenile salmonid ecology. A list of potential sources was developed through the contacts of the study team and later expanded to include the authors of papers located in the literature search and individuals that responded to our letters of enquiry. These contacts often led to further contacts and other sources of information.

All of these people were initially contacted by telephone. Generally the discussions were casual but where warranted a more formal interview was conducted.

INTERPRETATION AND ASSESSMENT

Initially a complex system was established to sort the information by species, geographic location, freshwater, estuarine or early marine life history stage and by the observational or manipulative nature of the work. As the study progressed, it became evident that there was not enough data to support such a scheme and that a simpler approach was required.

Literature, observations, and individual suggestions collected during the literature review and interviews were cross referenced by species and subdivided by their nature (either observational or manipulative). Those studies containing either experimentally derived information or information particularly relevant to enhancement in British Columbia were summarised in a case history format. These case histories are on file with Mr. D. Radford in the Vancouver office of the DFO Regional Planning and Assessment Branch. Together with the remainder of the data these case histories form the basis of the discussion section of the report. Where data on enhanced stocks werenot available, evidence derived from wild stocks was used as a basis for discussion.

SPECIES AND THEIR ENHANCEMENT STATUS

COHO

In 1960's and 1970's most North American facilities producing coho released their fish as one year old smolts in the early spring . These smolts moved through river and estuary systems relatively rapidly and then out to sea. The interaction problems associated with these smolts were limited to predation on chum and pink stocks migrating at the same time. Although this 'classic' coho problem was of concern, in many cases it could be resolved through altered release times (Johnson, 1974: Aimes in prep, pers comm).

Over the last decade, however, both the number of coho producing facilities and the number of production strategies increased. In addition to major facilities, coho are now produced by satellite hatcheries on smaller systems, incubation boxes, estuarine net pens and accelerated rearing in facilities operating with warm water. Age and size at release now varies from the unfed fry released from incubation boxes to the 2+ smolts released from a few major facilities. In addition, coho are released as fry after 20 - 60 days of hatchery rearing or as 0+ smolts after accelerated rearing. During the same time period outplanting techniques evolved that permitted the acclimation of coho juveniles in previously barren, under-utilized, or inaccessible habitats. In British Columbia a total of 10,400,000 coho juveniles were released in 1983 (Anon, 1985).

Most of the new fry rearing and release strategies are based on the premise that animals grown in the wild will reduce costs and increase the numbers and quality of the fry. In a production sense these assumptions may be valid, however, it is also true that increased time in freshwater increases the probability of interactions with other fish (either enhanced or wild stocks).

CHINOOK

In British Columbia enhancement facilities, coastal chinook are generally released as 90 day smolts; whereas interior stocks are released as either as 1-3g fry or occasionally as one year old smolts. In 1983 a total of 25 million juveniles were released (Anon, 1985).

Until recently, coastal chinook were thought to emerge in the early spring and spend a few months to a year in freshwater before migrating to the sea. In contrast, interior populations were thought to migrate mainly as one year old smolts. In the last decade, however, it became clear that the life history patterns of chinook were more complex than previously thought. In many coastal populations large numbers of newly emerged fry migrate directly to estuaries (Healey, 1980) and many interior populations exhibit several patterns of downstream migration (e.g. a spring fry migration; a fall presmolt migration, and a spring presmolt migration (Bjornn, 1978)). These complex patterns of migration make it difficult to generalize about interactions between chinook and other juvenile salmonids.

SOCKEYE

Sockeye salmon enhancement programs have been conducted with varying success in British Columbia since 1894 (Foerster, 1968). Most of the early operations depended on conventional incubation techniques and met with indifferent success. This approach now accounts for only a small proportion of the sockeye enhancement in B.C. In the last thirty years two additional techniques were adopted that appear to be more successful. The first, the spawning channel, provides a controlled incubation environment and decreases losses due to predation, scouring, siltation and freezing. Such channels usually are constructed adjacent to nursery lakes that are not producing to capacity. The intention is to increase the number of seaward migrating smolts. The second enhancement technique, lake enrichment, increases nutrient levels and thus the productivity of lake systems. Here the intention is to increase the size and survival of sockeye smolts. In 1983, the Salmonid Enhancement Program facilities in British Columbia released 131.6 million fry from spawning channels, 38.5 million through lake enrichment, and 1.8 million through a variety of hatchery techniques. An additional 60.6 million were produced by spawning channels operated by the I.P.S.F.C. (I.P.S.F.C. 1984).

CHUM SALMON

In most British Columbia river systems naturally spawned chum fry leave their incubation areas shortly after emergence and migrate downstream. They then remain in estuarine and nearshore areas for some time before moving offshore (Neave, 1966; Healey, 1979; Levy et al., 1979). Approximately 119 million chum fry were released in 1983 (Anon, 1985) and although an increasing number of enhancement facilities rear their chum fry for a few weeks before release, these hatchery reared fry apparently follow the same general migration pattern as wild fry. Given this life history, interactions between chum fry and other juvenile salmonids can be divided into two types: i) predation by resident species, or smolts, on chum fry, and ii) competition between chum and other migrating fry, particularly pink salmon, for food.

The migrations of unfed fry released from enhancement facilities are similar to those of wild stocks. In wild stocks, predation during freshwater, estuarine and early marine migrations has long been a source of concern to managers. Predation on chum fry is well documented and because the predators are thought to be swamped by the large numbers of migrating fry, predation losses are considered depensatory (Neave, 1953). Such losses, however, are not always depensatory. Hunter (1959) noted that proportional losses were up to four times larger during years of low fry abundance than during years of high fry abundance. Further analysis of Hunter's (1959) data by Peterman and Gatto (1978) suggests that in most years predators operate at the low, linear end of their functional reponse. Thus, prey levels are usually well below those that would swamp the predators capacity to consume fry.

The vulnerability of chum salmon fry to predation is related to their size. Hyama et al. (1972) and Fresh et al. (1980) found that losses during freshwater migration could be reduced by over 50% by not releasing the fry until their mean size was equal to, or greater than, 50mm.

PINK SALMON

In most of British Columbia, pink salmon enhancement has not received much attention, although in the lower Fraser River pinks have been enhanced since 1955 (Houston and MacKinnon, 1956). The 1983 releases totalled only 2.9 million fry (Anon, 1985) from a variety of incubation boxes and tray systems. In even numbered years this number is typically increased by 23.5 million fry from I.P.S.F.C. spawning channels on the Fraser River plus 1.5 million from DFO channels.

Like their wild counterparts, fry proceed directly to sea upon emergence. Although short term rearing is common in other areas (Dudiak, 1981), only 420,000 fry out of the millions released in British Columbia in 1982 were held in fresh or salt water before release. Their brief stay in freshwater means that, like chum fry, the interactions among juvenile pink salmon and the young of other salmonid species fall into two categories: either predation on pink fry by smolts and resident species or competitive interactions with other pink stocks and chum salmon.

STEELHEAD

Steelhead trout have been cultured in British Columbia and the Pacific Northwest for over two decades and rainbow trout have been stocked throughout the province since at least the 1930's. Usually, rainbow are stocked as fingerlings or yearlings, and steelhead are released as smolts. In 1983 steelhead culture in the province produced 2.2 million juveniles. An adult return of 55,600 is expected from this production (Anon, 1985).

The survival of cultured steelhead from juveniles to adults typically is lower than that found in wild steelhead. In Washington, about 2-7% of the cultured smolts survive to become adults (Wagner et al., 1965; P. Slaney, pers. comm.), while in B.C. survival rates for large, cultured smolts are around 4-5% (Hooton and Hay, 1978; Slaney and Harrower, 1981). In contrast, wild steelhead trout in B.C. exhibit survival rates of 8-15% (Slaney et al., 1982).

In recent years, the costs of steelhead culture has increased substantially. This increase is primarily due to the practice of heating water to increase incubation and growth rates. This cultured method produces large smolts and thus increases the survival rate (Wagner et al., 1963; Hooton and Hay, 1973). With the inception of the federal Salmonid Enhancement Program in 1977, cost-effective alternatives to hatchery rearing were sought, and provincial biologists have investigated both lake net-pen rearing and headwater stocking of fry as alternatives. Survival to adult size of juveniles released from such enhancement alternatives varied from similar to other culture methods to greater than wild smolt survival.

Steelhead are generally spring spawners (March to May) regardless of whether they are winter or summer run fish. The young emerge from the gravel during mid-summer (June or July) and the juveniles rear in freshwater for one to four years before migrating to sea.

They reside in the sea for an additional one to four years (Pautzke and Meigs, 1940; Withler, 1966) before returning to freshwater to spawn. Withler (1966) noted that B.C. steelhead tend to reside longer in both freshwater (3 years) and the ocean (mostly 2-3 years).

Usually interactions between juvenile steelhead or rainbow and other salmonid species are limited to freshwater, especially riverine habitats. Migration through estuaries is during mid-April to early June and is generally brief (Loch, 1982). This limits estuarine interactions. During early marine life the main interaction is steelhead predation on juveniles of their species.

CUTTHROAT

Both wild and hatchery-reared juvenile cutthroat trout probably interact as competitors and predators with other salmonids. During their stream residence, cutthroat compete for food and space with stream rearing species such as coho and steelhead. At larger sizes cutthroat trout become piscivorous and are potentially predators on all juvenile salmonids. In British Columbia anadromous cutthroat trout usually are released as one year old smolts of 70 - 130g weight (D. Peterson, B.C.F.W. Fraser Valley Trout Hatchery). In addition, surplus stock is occasionally released at 1.5 - 2.0g. These smaller fish may spend one or more years in small tributaries and headwaters before migrating. The larger smolts normally migrate to sea shortly after they are released. Cutthroat, however, typically stay in the sea for only a short period and often return to freshwater in the same year that they migrated to sea (Jones, 1973; Giger, 1972). Some fish apparently overwinter in estuaries (Lucas, 1979) and in some rivers, such as the Fraser, cutthroat may not travel beyond the river's estuarine plume (A. Tautz, B.C.F.W. pers comm.). British Columbia hatcheries released 94,121 cutthroat juveniles in 1983 (Anon, 1985)

EVIDENCE OF INTERACTIONS

INTRASPECIFIC INTERACTIONS

Intraspecific Competition

Coho

Beyond basic questions concerning habitat rearing capacity, the primary interactions among coho stocks are competition for food space in freshwater and the possibility of competition for food among 0+ smolts in estuaries.

Using an artificial stream, Glova (1978a) demonstrated that the behaviour of wild coho fry differed from that of hatchery fry. Wild fish quickly partitioned food and space through the mechanisms of territoriality and dominance, and once established, their social positions were relatively stable. Thus, the dissipation of energy through social interactions was reduced. Hatchery fish, in contrast, tended to school. Apparently the major result of imposing hatchery coho on a wild stock was that they disrupted the spatial and social distribution of resident fish. This disruption might jeopardize the growth and survival of the wild stock. Glova suggested minimizing the period of hatchery rearing before outplanting and argued that this would reduce the behavioural differences between the wild and hatchery stocks and thus decrease the disruptive effect.

The importance of size at release and hatchery rearing time was also emphasized by Solazzi et al. (1983). Their study was designed to investigate the effectiveness of stocking streams to increase the density of coho juveniles rearing in Oregon coastal streams. They found that planting hatchery coho resulted in a 40 - 50% decrease in the density of wild coho. The streams were stocked in April and May and in August. When rearing densities were examined, hatchery fry were 70 - 90mm in length whereas most wild fish were 40 - 70mm in length. They suggested that the wild fish were displaced by the larger hatchery coho. The hatchery fry had emerged earlier and thus had a two to three month period of feeding before they were stocked. Solazzi et al. concluded that the density of coho salmon at the end of the summer rearing period could be increased by stocking hatchery fry, but that it would be necessary to use a donor stock whose spawning and emergence times were close to those of the wild stocks in the target streams.

Myers (1978, 1980) investigated food and space use in wild and cultured coho, chum and chinook salmon in estuarine habitats at Yaquina Bay, Oregon. She found that the temporal and spatial distributions of wild stocks did not overlap and suggested that some resource partitioning was in effect. When the diet and distributions of hatchery released coho were examined, however, there were few differences between the hatchery and wild coho despite gross differences in their growth patterns and life history (hatchery fish were 0+ at estuary entry vs 1+ in the wild stocks). Further, because of their large numbers (over 9 million per year), hatchery fish outnumbered all other species during some periods of the year. Thus, although no estimates of estuary rearing capacity were made, and no hard evidence for interaction was presented, it was suggested that the potential for competitive interactions existed and that the timing of hatchery releases should be adjusted to avoid conflict with the wild stocks. Perhaps a similar potential for interaction occurs in early marine life history stages.

Chinook

The evidence for intraspecific competitive interactions among juvenile chinook in freshwater is fairly clear. Bjornn (1978) demonstrated an inverse relationship between smolt size and population size in chinook in the Lemhi River, Idaho. There were three classes of down-stream migrants in this system: fry; pre-smolts and smolts. Because the proportion of migrants in the three classes remained virtually constant over a sevenfold change in total density, this decrease in smolt size as population size increased implies intraspecific competition.

Similarly, Lister and Walker (1966) noted two periods of downstream migration from the Big Qualicum River and argued that, since the output of late migrants was relatively small and constant compared to a large and variable fry migration, the size of the fry migration was probably density dependant. Again, this implies an intraspecific interaction - in this case competition for stream rearing space - and the agonistic behaviours reported by Reimers (1968) seem to provide possible causal mechanisms.

Sockeye

Like wild sockeye, enhanced stocks probably interact with other sockeye primarily through competition for food. As numbers increase there are density dependant decreases in growth and survival (Foerster, 1968). No evidence for changes in wild stocks as a result of enhancing stocks could be found during the present review and, where spawning channels are installed to take advantage of clearly underutilized rearing capacity, such interactions are unlikely. In lake enrichment projects the situation is not clear and little data was available; however, if several stocks use the same rearing lake and they differ in emergence time it is possible that the timing of lake fertilization may influence the natural balance between stocks.

Chum

No well documented evidence of intraspecific competition in juvenile chum salmon was uncovered by our review. In chums migration from freshwater areas probably is quick enough to minimize interactions in freshwater. There is, however, some evidence to suggest that intraspecific competition may occur in estuaries and nearshore rearing areas. Apparently, chum salmon are efficient foragers in these nearshore areas and are capable of rapidly depleting localized populations of their preferred epibenthic invertebrate prey (Sibert, 1979; Healey, 1979; Simenstad et al., 1980). Although the exact mechanism that governs the shift in chum juveniles from epibenthic to water column prey is not understood, prey depletion appears to be an important factor in their movement offshore. Simenstad et al. (1980) have suggested that shorter rearing times and increased migration rates that result from prey depletion may be responsible for reducing the marine survival of chum salmon. Given that estuarine rearing capacities are finite, then the introduction of large numbers of chum juveniles into areas already supporting large numbers of wild or enhanced chum juveniles could result in intraspecific competition.

Pink

Simenstad (1980) suggested that increasing the numbers of chum fry in Hood Canal may shorten their residence times and thus lower survival. The same is probably true of pink salmon. Thus large releases in relatively confined areas might exceed the area's rearing capacity; however, there was little data to confirm this point and estimates of nearshore carrying capacities are confounded by irregular plankton distributions, tidal flux and variations in feeding behaviour (Cooney et al., 1978; Simenstad et al., 1980).

Steelhead

Rainbow trout can be aggressive and territorial, especially if food abundance is low (Slaney and Northcote, 1974). In addition, intraspecific, and even intracohort interactions, probably inhibit growth and survival in trout more than interspecific interactions (Fraser, 1969; McFadden, 1969). With the increased stocking of smolts in mainstem areas and an apparent increase in residualism, the potential for intraspecific interactions affecting growth and survival of wild and cultured trout is high.

The literature on the interaction of cultured and wild steelhead and rainbows is somewhat contradictory. Generally, although cultured fish appear to be genetically less heterozygous and thus less 'fit' (Reisenbichler and McIntyre, 1977), where competitive interactions occur, wild rainbows show increased dispersal and decreased survival.

There is some indication that cultured trout occupy different microhabitats than wild trout (Allee, 1981). Johnson (1981) studied dietary overlap between hatchery rainbow and wild rainbow in the Salmon River, N.Y. and concluded that overlap is not significant. Wild trout selected a diverse range of prey, whereas hatchery trout tended to select epibethic prey. Such studies suggest that intraspecific interactions between cultured and wild trout are minimal; however, in each of the above studies habitat diversity and prey availability appear to have been high. Interactive effects would be more evident in more restrictive environments.

Hochachka (1961) noted that stocked hatchery trout showed lower liver glycogen levels for 2-3 weeks after stocking than wild trout. This might make them less efficient at feeding than wild animals. Over a longer period, however, Bjornn (1978) showed that the stocking of steelhead trout in Idaho rivers adversely affected resident rainbow abundance. Before stocking, wild rainbows accounted on average for 75% of the fish present. After 10 years of stocking, only 10-20% of subyearling trout were resident rainbow, and older resident trout had dropped from 44% to 6-16% of the salmonid population. These results agree with Jenkins' (1971) assertion that, since hatchery trout do not show the typical social density regulation and dispersal mechanisms of wild fish, wild trout can be overcrowded or displaced under stocking conditions. Slaney and Harrower (1981) contend that repeated releases of cultured steelhead smolts lead to standing crops of residuals that exceed the natural carrying capacities of streams. The only period over which cultured trout may be at a disadvantage is winter. In Convict Creek, California, Reimers (1963) observed that hatchery rainbow trout showed higher winter mortalities than wild fish and that wild fish were generally hardier over this season than hatchery fish. Thus, although cultured fish appear physiologically less fit on release and potentially less fit genetically, in most instances competitive intraspecific interactions favour cultured fish to the detriment of resident rainbow or steelhead. This is particularly so at high densities.

In estuarine and marine habitats, intraspecific competitive interactions may occur but they are probably minimized by the wide range of foods available.

Intraspecific Predation

Coho

In circumstances where coho are concentrated due to natural or artificially manipulated flow conditions, cannibalism has been observed both among and within year classes (E. Perry, DFO pers comm). This type of type of interaction is unusal, however, and there are no data to suggest it has a significant impact on coho stocks.

Chinook

There is no suggestion in the literature of strong intraspecific predation in chinook salmon; however, indirect evidence suggests that cannibalism is possible, especially in interior populations such as the upper Columbia River where newly emerged fry and smolt-sized juveniles are briefly present in the same localities at the same time. The only record of chinook smolts preying on chinook fry is from an interior system (upper Yakima River), although in this case it was not clear that the predators actually were chinook smolts (Patten, 1972). Certainly, chinook yearlings will prey on salmonid fry (Northcote et al., 1979) and such observations suggest intraspecific predation is possible; however, it does not appear to be common. Perhaps, because chinook juveniles show size related current preferences (Lister and Genoe, 1970), the different size classes are segregated even within a local area.

Sockeye

No evidence of intraspecific predation was found.

Chum

No evidence of intraspecific predation was found.

Pink

No evidence of intraspecific predation between juvenile pink salmon was found; however, some evidence suggests that there may be predation between year classes (Dudiak, 1984).

Steelhead

Predation by larger yearlings or older steelhead on sub-yearling trout is possible. The literature, however, suggests that cannibalism even under high density conditions is not a problem (Fraser, 1969; Chapman and Quistorff, 1938). Stauffer (1977) calculated regressions between yearling and age 0 rainbow trout in Lake Superior tributaries. None of the regressions were significant, suggesting the absence of an effect of yearlings on sub-yearling trout.

Cutthroat

No evidence of intraspecific predation was found.

INTERSPECIFIC INTERACTIONS

Interspecific Competition

Coho

During their freshwater rearing period coho may interact competitively with any of the other juvenile salmonids that use similar habitats. Thus there is a potential for interactions at various life history stages with chinook, sockeye, steelhead and cutthroat; whereas, the life history pattern of chums and pinks generally keep these species separate from coho.

In coastal British Columbia, interspecific competition between coho and chinooks is of limited importance. Where the two species occur together during freshwater residence, size differences appear to produce spatial segregation based on current velocity (Lister and Genoe,1970). This spatial segregation, however, may be due in part to interaction between the species. In Oregon, fall chinook and coho appear to interact competitively (Stein et al., 1972) and a comparison of microhabitat use by juvenile chinook in the presence and absence of coho is sorely needed. No evidence for interactions during the estuarine and early marine life history stages was uncovered during the review.

The literature search uncovered little evidence of competitive interactions between enhanced stocks of coho salmon and juvenile sockeye; however, recent work by Jeff Koenings (F.R.E.D. Alaska Dept. Fish and Game) suggests that there may be competitive interactions between coho and sockeye juveniles in some Alaskan lakes. There, coho introduced into barren lakes developed limnetic habits, whereas coho introduced into sockeye lakes remained in the littoral zone. This type of interaction does not appear to occur in British Columbia and it has been suggested that this difference may be due to the more structured nature of both littoral zones and zooplankton populations in most coastal B.C. lakes (K. Hyatt, pers comm.). Additional work on coho-sockeye interactions in Alaska was recently completed by R. Wilmot (U.S.F.W.S., Anchorage) The results, however, are not yet available.

Milne (1948) in a review of coho and steelhead biology noted that these species have similar geographic ranges, meristic counts, spawning locations, breeding changes, feeding habits and the lengths of time in freshwater. Griffith (1980) also noted that both species, particularly the sub-yearlings, use similar freshwater microhabitats. This suggests that the potential for competitive interactions between these species in freshwater is high, and that such interactions could influence the numbers, growth, or survival of both species.

Hartman (1965) observed that although the distribution of juvenile coho and steelhead in streams was similar, their microhabitat distributions were quite different in spring and summer. In the summer coho tend to occupy pools while steelhead are found in riffles. Hartman (1965) inferred that this segregation was the product of intense aggression and resulted from similar environmental demands by the two species and high population densities. Stream channel experiments suggested that each species more aggressively defends the habitat it preferentially selects in nature. In the winter both species occupy slow velocity pools and refrain from aggressive interactions. Hartman (1965) attributed this low interaction period to lower winter densities and reduced ecological demands. Fraser (1968, 1969) used modified rearing channels at Robertson Creek, B.C. to study steelhead-coho interactions and concluded that they have evolved species-specific differences in growth rates and survival. Thus interactions are limited by different spawning and emergence times that allow temporally different habitat use. Fraser (1968, 1969) observed that different emergence times initially limited interspecific interactions but that both survival and growth were primarily affected by intraspecific interactions.

Coho juveniles emerge earlier in the spring than steelhead and are therefore at an ecological advantage. However, in coho, survival and growth are so strongly affected by intraspecific aggressive interactions that although steelhead emerge later they grow faster and by autumn have overcome the early size advantage of coho. Thus coho survival may be affected by steelhead, but only if steelhead densities are high. Taube (1975) and Stauffer (1977) noted that in the summer months under natural densities subyearling coho and rainbow trout do not exert a detectible influence on each others growth or survival.

Bustard and Narver (1975) studied interactions during winter residence in pools in Carnation Creek, B.C. Although both species occupied low velocity waters, coho (1+) were found under cover in shallow peripheral areas especially sidechannels and bays; whereas steelhead (1+) were usually found in more open water and closer to the bottom. Fry (0+) of both species used shallow water (<15 cm depth) of low velocity (<15 cm/sec) but steelhead were more closely associated with rubble than coho. Bustard and Narver conclude that winter survival in steelhead was closely associated with the availability of substrate cover. Survival in Carnation Creek, where most rubble was less than 15 cm in diameter, was much lower (6%) than that found by Hartman (1965) and Everest (1969) in streams with larger rubble (20-40 cm, and 40 cm).

Food studies (Peterson 1966, Johnston 1967, and Fraser 1968) indicate that while coho and steelhead have similar diets, food overlap is limited by vertical segregation. Coho feed on drift organisms and at the water surface whereas steelhead feed on more benthic prey. The potential for competition, however, does exist, particularly at high densities or under conditions of restricted food abundance (Wagner, 1975). In a laboratory experiment on 0+ coho and steelhead interactions Laarman (1969) noted that a restricted food supply resulted in depressed coho growth. He suggested this might be because of the high energy requirements of coho agonistic behaviour.

Allee (1981) concluded that in riverine habitats, juvenile coho and steelhead are segregated initially by different emergence times and subsequently by subtle habitat partitioning. Regardless of size, coho initiate interactions and are agonistically dominant to steelhead; however, interactions are usually restricted to situations of high density and low food availability. Under these conditions, steelhead may be displaced from preferred habitats but coho appear to sacrifice growth, and to some extent survival, to maintain the high energy costs of aggressive behaviour.

Given that enhanced steelhead behaviour is similar to wild fish behaviour, stocked steelhead fry or smolts can be expected to interact with coho to a limited degree. Interaction levels will probably rise with densities, and coho juveniles should respond with lower growth rates and survival. Interestingly, Allee (1981) observed that large hatchery steelhead do not select bottom habitats or prefer benthic foods but appear to occupy a position in the water column intermediate between wild trout and coho. They also use a wider variety of prey than wild trout. There is, therefore, a greater potential for interaction between cultured trout and coho than between wild trout and coho. Enhanced coho also can be expected to interact with steelhead in areas of high densities. In most cases, however, release timing, size differences, and limited numbers of wild steelhead juveniles should minimize competitive interactions.

One result of stocking coho fry into previously inaccessible headwaters or other unoccupied habitats appears to be the displacement of resident cutthroat trout. In many cases, this results in lower growth and survivals rates in the trout. Recent work in British Columbia (Tripp and McCart, 1983, and de Leeuw, pers. comm.) confirms the concerns expressed by Glova (1978a and 1978b) and Glova and Mason (1977a and 1977b). These authors reported that coho fry tend to displace cutthroat trout from preferred habitats, and that this effect is more marked when the introduced coho fry are hatchery reared.

Glova (1978a) examined the interactions of both wild and hatchery coho fry with cutthroat trout taken from populations resident above falls. Working in a stream simulator, he found that wild stocks of coho and cutthroat trout rapidly partitioned available stream space through the mechanisms of territoriality and social dominance. Once established, the social regime appeared stable, with coho usually dominant in pools and trout dominant in riffles. When hatchery coho were introduced along with wild trout, schooling behaviour on the part of the coho minimized one-to-one interspecific encounters. The result was that even the largest trout often were unable to establish territories. Thus the trout became nomadic and encountered reduced feeding opportunities.

Glova repeated these experiments in a small experimental stream channel stocked in advance with cutthroat trout. He obtained similar results except that in the stream trout survival was reduced from that of the controls by about 40%. This decrease in survival appeared due to increased predation that occured as a result of displacement from cover in the pools. Upstream migration of cutthroat also increased when coho were added to the test channel.

Tripp and McCart (1983) investigated the feasibility of planting surplus hatchery coho fry into inaccessible headwaters. They reported that isolated cutthroat populations were adversely affected by such introductions. Their results are difficult to interpret because of inconsistencies between the two study streams, a lack of dividers between experimental and control stream sections, and difficulties in accurately censusing cutthroat early in the year. Densities of cutthroat young of the year, however, clearly declined in areas where coho were stocked even though no relationship between stocking density and cutthroat density was observed. In control (unstocked) areas survival over the study period exceeded 100%. This indicates some immigration from other areas. Older cutthroat were also affected by coho outplants and in this case the magnitude of the effect increased with stocking density. Also, as Glova (1978) suggested, the growth of cutthroat trout was adversely affected by the coho stocking. This effect was greatest when coho were stocked early in the year and at high densities.

Coho may not interact directly with young of the year cutthroat but rather with one and two year old fish. de Leeuw (pers. comm.) reports that in tributaries of Mosquito Lake on the Queen Charlotte Islands, substantial declines in the density of cutthroat trout were associated with coho introductions. Minnow trapping and electrofishing in unstocked streams in this system revealed that cutthroat young of the year were found mainly in riffles whereas one and two year old fish occupied pools. In areas where coho were stocked, the distribution of young of the year did not change; however, the one and two year old fish were apparently displaced from the pools and this habitat was exclusively occupied by coho.

Chinook

The wide variety of chinook life history patterns increases the potential for interacions with other juvenile salmonids. In systems with 'stream type' chinook, there is the potential for interaction with other freshwater rearing species. Alternately, 'ocean type' chinook smolts could interact with other salmonids in estuarine and inshore marine habitats.

Competitive interactions between juvenile chinook and coho were discussed in the previous sections. Other freshwater interactions, including those with steelhead and cutthroat trout, are discussed below. The potential for competitive interactions between chinook and chum in estuarine environments is also discussed. No evidence for competitive interactions between juvenile chinook and sockeye or pink salmon was found.

Although firm evidence for competitive interactions between chinook and chums could not be found, it is possible that such interactions occur in estuaries. In many systems, estuarine rearing by chinook and chum overlap and there is some evidence that the two species occupy different portions of estuarine tidal channels (Levy et al., 1979; Levy and Northcote, 1982). Chum are smaller than chinook, yet there is often considerable overlap in their diets, especially early in the year. On the Nanaimo estuary, Healey (1979, 1980) found that chinook juveniles appeared to stop preying on small invertebrates, such as harpacticoids, about the same time as chum appeared in the estuary and began to consume these invertebrates. There is no evidence, however, that this diet shift is the result of an interaction with chums and perhaps the chinook simply outgrew these prey items.

Competition between chinook and steelhead juveniles is a potentially important interaction. The freshwater rearing areas used by both species appear similar, and Bjornn (1978) demonstrated that steelhead production (measured in the yield of migrants from a given number of fry) decreased when chinook were added to a system. This certainly suggests interspecific competition and it is unlikely that only the trout were affected. The potential for interaction between juvenile chinook and rainbows appears to be particularly high in interior systems. Slaney et al. (1977) reported large numbers of chinook and rainbows coexisting in upper Fraser drainages. Again, a study of microhabitat use by juvenile chinook in the presence and absence of rainbow trout is needed.

As with freshwater interactions between steelhead and coho, steelhead and chinook are initially segregated by size differences that are a product of different emergence times. Both species apparently use the same microhabitats and segregation between sizes classes is both intra and interspecific (Everest, 1969). In spring, chinook emerge and take up positions in shallow, low-flow areas. As they grow, chinook fry move into progressively faster and deeper waters. Steelhead emerge later (June to July) and occupy the same shallow low-flow areas, now abandoned by chinook; however, steelhead prefer substrates with more rubble than chinooks. Again, with growth, the steelhead move into faster and deeper water usually over larger rubble. In Idaho streams, Everest and Chapman (1972) observed both chinook and steelhead fry (0+) in water velocities of <0.15m/sec and depths of <0.3m.

The progressive shift of both species to higher water velocities apparently is food related. Such waters contain higher drift food densities per unit time than low-flow areas (Everest, 1969). Within each size grouping fry densities are socially controlled (Chapman and Bjornn, 1969). In the late summer, as streamflows decline, velocity becomes progressively less of a controlling factor in habitat use. When the water temperature drops below 5°C both species move down into larger streams where they take up positions close to the bottom and use the substrate as cover. At this time the opportunity for interspecific competition between steelhead and chinook probably is maximal; however, low digestion rates and adequate food appear to keep natural interactions to a minimum (Chapman and Bjornn, 1969).

None of the material reviewed examined diet overlap in steelhead and chinook. Chinook generally feed on drift organisms (Chapman and Bjornn, 1969), whereas steelhead feed on both drift and benthos. Thus, although their diets probably overlap, these foraging differences have the potential to reduce overlap at times of low food abundance.

From the information available on wild, sympatric populations of steelhead and chinook it appears that the potential for interactions between enhanced stocks in freshwater is high. Especially if the stocked steelhead are of a size similar to the chinook fry. Steelhead appear to be more stereotyped in their behavioural responses and habitat requirements than chinook and therefore may be interactively subordinate to chinook (Everest, 1969). Thus, because both species use similar habitats, steelhead could be adversely affected by chinooks. Bjornn (1978) examined production of steelhead, rainbow and chinooks stocked in sections of streams in Idaho and found that although overall fish production increased (from 16.3 g/m^2 to 26.9 g/m^2) in sympatric situations, sub-yearling steelhead-rainbow production dropped substantially (9.6 g/m^2 to 4.3 g/m^2).

Competitive interactions between steelhead and chinook in estuarine and marine habitats are unknown. Predation by steelhead on chinook fry, however, has been examined in estuarine, inshore and oceanic habitats. In both the Columbia River estuary (Loch, 1982) and Puget Sound (Fresh et al., 1981), steelhead fed on gammarid amphipods, insects, and other invertebrates. The only fish consumed were herring larvae (Fresh et al., 1981). In the marine environment, however, steelhead fed preferentially on fish. Loch (1982) found steelhead (203-240.9 mm TL) had up to 40% fish material in their stomachs. This material included an identifiable chinook fry (83 mm TL). Fresh et al. (1981) examined 16 steelhead (380± 49 mm FL) taken in the open ocean off Washington and found that chinook fry made up 33% of the fish biomass in their stomachs. Thus, steelhead can be expected to feed on chinook fry in marine waters; however, in estuaries steelhead predation does not appear to be a problem. Perhaps the brief migration through the estuary and abundant alternate food sources minimizes predation in estuaries.

Sockeye

A lacustrine freshwater habitat and rapid transit through estuaries is typical of most sockeye stocks and tends to minimize their potential for competitive interactions with other juvenile salmonids. An exception, may be the lake rearing populations of coho discussed previously. These populations appear to show some competitive interactions with sockeye in some Alaskan systems.

Chum Salmon

The brief freshwater residence of chum salmon minimizes opportunities for competitive interactions between chum fry and other juvenile salmonids. In estuaries, however, there are indications of competitive interactions between chum fry and ocean-type chinook. In addition, although manipulative, or experimental data, on interactions between juvenile chum and pink salmon are not available, there are strong indications that these two species may compete for food and in some instances the presence of pink salmon may decrease predation on chum fry.

Competition between some chum and pink salmon stocks appears to be for estuarine and early marine food resources. Johnson (1979), Gallagher(1980 and Aimes (in prep.) have hypothesized that such competition may be responsible for the distinct odd - even cycles in natural chum populations in Washington. In this state, chum stocks that are geographically relatively distant from any pink stocks, show distinct odd - even brood years with marked differences in survival. The brood years that coincide with pink broods have lower survival than those that occur on pink off years. On the Washington Coast, the odd year survival rate is less than 50 % of the survival rate on even years. In Puget Sound the difference varies from 63.4% in the north to 50.2% in the south (Stone, 1983).

In Hood Canal, Simenstad et al. (1980) examined the food used by outmigrating pink and chum salmon. They noted not only a dietary overlap of up to 84%, but also that the large numbers of juveniles moving through the inlet were sufficient to deplete standing crops of the preferred epibenthic and neritic inverterbate prey. Together these lines of evidence strongly suggest that these species compete for food in restricted near-shore areas.

Pink

Pink salmon are characterized by a rapid downstream migration after emergence and a rapid transit through estuarine habitats on the way to near-shore, marine rearing areas. Thus, beyond the possibility of competitive interactions with chum fry in estuarine and nearshore nursery areas (see discussion in section on chum salmon), no references to competitive interactions involving pink fry were found during the review.

Steelhead

In previous sections possible competitive interactions between juvenile steelhead and other stream dwelling juvenile salmonids, including coho and chinook, were discussed. Not suprisingly, there is little evidence of competitive interactions with non-stream dwellers such as sockeye, chum and pink salmon. Steelhead and cutthroat trout coexist in many stream and lakes in British Columbia, and given similar emergence times, competitive interactions between these species may be a problem. Generally, however, the two species of trout appear to segregate spatially in both riverine and lake habitats.

In southwestern B.C., Hartman and Gill (1968) concluded that segregation in stream systems is longitudinal. Steelhead are more abundant in the lower reaches of streams, while cutthroat inhabit small tributaries and headwaters. In allopatric situations, juvenile steelhead were either found in large streams (drainage areas >130 km^2) or in smaller, steep-gradient streams flowing directly into the sea. In contrast, smaller streams (<13 km^2) that dropped steeply but then levelled off and flowed slowly through lower reaches and sloughs were favoured by cutthroat. Griffith (1980) noted that in sympatry small cutthroat prefer slightly shallower, faster waters over larger substrates than steelhead, whereas older cutthroat select somewhat slower water over a more mixed substrate than similar sized steelhead. Both rainbow and cutthroat feed on a mixture of drift, epibenthic invertebrates and fish. In the Cowichan River system, Idyll (1942) observed that although rainbow and cutthroat overlap in diet, cutthroat generally were more piscivorous.

Nilsson and Northcote (1981) examined 17 allopatric and 10 sympatric lake populations of these trout in B.C. In allopatry, both species used a wide range of prey and habitat types. In sympatry, however, rainbow trout were more limnetic and planktivorous whereas cutthroat were more littoral and piscivorous. Also, growth (size at specific ages) in sympatric cutthroat was higher than in rainbows. This situation was reversed in allopatry. In laboratory behaviour experiments rainbow were more aggressive than cutthroats and perhaps in sympatry they divert more energy from growth into agression (Nilsson and Northcote, 1981). Where behavioural interaction occur between these species, steelhead are dominant.

Both cutthroat and steelhead smolts and older cutthroat are found in estuarine and marine waters. In estuaries migratory juveniles of both species feed heavily on insects and gammarid amphipods. In marine waters both species feed on fish and crustaceans (Loch, 1982). Fresh et al. (1981), however, believe that there is little dietary overlap between the species and that cutthroat are mostly piscivorous.

Cutthroat

Cutthroat typically rear in freshwater for two years before migrating seaward. During this period as discussed previously, there is a strong possiblity of competitive interactions between this species and coho and possibly steelhead fry. Juvenile chinook and sockeye appear to be separated from cutthroat by habitat preferences (Griffith, 1980 MS). Size differences make it unlikely that cutthroat interact competitively with chum and pink fry in estuaries.

Interspecific Predation

Predatory interactions among juvenile salmonids appear to be size mediated (Parker, 1965; Bams, 1967; Taylor and McPhail, 1984). This suggests that there is the potential for predatory interactions wherever large juveniles or smolts are released in the presence of smaller juveniles or fry, and where fry are released in the presence of larger fish.

Coho

In British Columbia, coho are commonly released in the spring as 2g fry, and in the fall as 5g fry, or in the spring as yearlings (DFO file data). Because of this size range and the differences in the duration of freshwater rearing, coho are both predators and prey in interspecific interactions. Predation by coho smolts on salmonid fry decreases as fry size increases (Bams 1967; Taylor and McPhail, 1984). Since chinook fry are large relative to other salmonid fry, it is unlikely that chinook commonly suffer heavy losses from predation by coho smolts. There are numerous reports, however, of predation by wild coho smolts on sockeye fry both during fry migrations and lake residence (Ricker, 1941; Foerster and Ricker, 1941). Thus, there is some concern that sockeye stocks could be affected by increased coho enhancement activities.

In Scully Creek on Lakelse Lake, J. MacDonald (in Foerster, 1968) suggested that coho presmolts were the major cause of mortality in sockeye fry migrating to the lake. Between 1949 and 1953, the total numbers of coho, cutthroat, Dolly Varden and sculpins were estimated from fence counts and mark-recaptures. In addition, fry consumption rates were calculated from stomach samples and *in situ* digestion experiments. The results suggested that although individual coho took fewer sockeye than the other species, coho were numerous and therefore responsible for most of the sockeye losses. Total losses in the years 1950, 1951, 1952 and 1953 were calculated as 63%, 84%, 76% and 75% respectively.

In sockeye nursery lakes, coho do not appear to be as important predators as Dolly Varden, squawfish and cutthroat trout. They can, however, contribute to total sockeye losses. Ricker (1941) reported that coho stomachs from Cultus Lake contained sockeye juveniles in all months of the year. There was, however, a suggestion that coho did not prey on outmigrating sockeye smolts. This suggestion was based on the observation that the coho in areas downstream of the lake outlet contained only insects during the sockeye outmigration.

Wild stocks of chum and coho coexist in many rivers along the Pacific coast and coho smolts often prey heaviliy on chum fry during downstream migrations and in estuaries. Although this predation can result in severe losses of chum, the continued survival of natural stocks suggests that the predation rate is not excessive; however, in some areas the enhancement of coho stocks may upset a balance. Thus, chum salmon losses may increase either because of the presence of greater numbers of coho or through altered migration timing that may increase the time that chum salmon are exposed to coho predation.

The problem is perhaps best illustrated by Johnson (1974). He noted that the chum salmon populations in southern Puget Sound declined to 10% of their historic levels between 1960 and 1970. Yet production in other Puget Sound systems remained relatively constant. During this same period coho production in the area increased from 2,000 to 20,000 returning adults per year. Most of this increase was due to hatchery stocks released in early spring just before the migrations of the natural coho stocks. Apparently, these early coho releases increased the time chum fry were exposed to coho and this resulted in an increased level of predation. In recent years, coho have been released after the chum fry migration and the chum stocks appear to be recovering.

Predation by wild coho smolts on pink salmon has been documented by many authors (Pritchard 1936, Neave 1953, Hunter 1959 and Parker 1971). Apparently, in some cases, this problem has been increased in by enhancement activities. The key to avoiding this problem seems to be release timing and those same enhancement activites may provide opportunities to manipulate release times and reduce losses due to predation.

Parker (1971) reported that coho smolts began to prey on pink fry soon after the fry emerged. The coho followed the pinks downstream, through the estuary and for the first weeks of their marine life. Using a series of multiple mark-recapture experiments conducted as pink fry moved out of the Bella Coola River and seaward along Burke Channel, he calculated that fry losses were between 59 and 77% in the first 40 days after emergence, and that most of these losses were due to predation by coho smolts. Recently, Hargraves (pers comm) observed coho predation on pink fry in Masset Inlet and suggested that coho were the major cause of pink fry losses in their early marine life.

Models of coho smolt predation on pink fry were developed by Bailey (1974), Peterman and Gatto (1978) and Belford (1978). They suggest that coho predation can significantly affect pink fry survival and that the extent of predation can be influenced by the duration of exposure. Thus, delaying coho releases may be the easiest way to avoid negative interactions.

Aimes (in prep., pers. comm. investigated the decline of pink stocks in the Stilliguamish River. This river flows into the north end of Port

Susan, Washington. He found that this decline occurred when pink stocks were increasing in the rest of the state, and also that the decline coincided with a coho smolt release program at the south end of Port Susan. The coho were released in early May, a time when only 30% of the Stilliguamish pink fry migration was complete. Apparently the pink fry were unable to get out of Port Susan without severe mortalities from coho predation. In 1981, the coho release was delayed for three weeks to permit the pink salmon to migrate. Although more data will be required for a complete assessment, first returns indicate that the change was a success and that the returns of pinks to the Stilliguamish were up significantly in 1983. As noted earlier, delaying coho smolt releases appears to reduce this kind of interaction. Unfortunately, where other techniques, such as outplanting, are used it is not clear what the best way is to avoid predation. Based on experience with wild stocks, it appears likely that if smolts produced by outplanting migrate with the wild smolts, they will prey on pink fry and so could negatively influence pink stocks.

Predatory interactions between coho and steelhead are probably limited to predation by steelhead smolts (1+ or older) on coho fry because spring releases of coho are generally too early to allow coho predation on trout fry that emerge during summer. Patten (1972) studied wild stocks in 10 Washington streams found only limited predation by rainbow trout on coho juveniles as summarised below:

Coho salmon eaten by rainbow trout in Washington Streams during 1961 and 1962 (Patten, 1972)

System	Trout Sampled	Trout Size (TLmm)	% Stomachs containing coho	Coho per trout feeding on fry
Abernathy Ck	2	110-124	50	1
Hamilton Ck	6	68-147	16.7	1
Newautum R.	27	71-147	3.7	1
Raging R.	10	102-202	30.0	2

Chinook

Resident rainbow trout regularly prey on downstream migrant chinook fry (Patten 1971, 1972). The trout are large compared to chinook fry and thus the relatively large size of chinook fry is probably no advantage in this predator - prey interaction. Large trout, however, are usually few in number and their affect on chinook fry mortality is probably depensatory. In local areas, and for short time periods, hatchery reared steelhead smolts may inflict significant mortalities on migrating chinook fry. In the sea adjacent to the Columbia River estuary both Loch (1982) and Fresh et al. (1981) reported juvenile steelhead preying on juvenile chinook . Wild chinook smolts (>50mm) prey on other juvenile salmonids in the lower Fraser system (Northcote et al., 1979; Levy et al., 1979) and chinook >100mm appear to be largely piscivorous (Fresh et al., 1981).

Sockeye

Sockeye fry are commonly eaten by coho yearlings, rainbow and cutthroat trout, and Dolly Varden Charr (Ricker, 1941; Foerster, 1968; Meachum, 1977). Most of this predation occurs as the fry migrate from incubation areas to rearing areas. Losses during lake rearing may also be significant (Ricker, 1941). Smolts migrations in sockeye are relatively brief and little time is spent in either stream or estuarine habitats (Foerster, 1968; Levy et al., 1979). There is little evidence of predatory interactions with other salmonids during this phase of their lives.

Ginetz (1972) and Ginetz and Larkin (1976) studied rainbow predation on migrant sockeye fry in the Fulton River system, Babine Lake, B.C. They observed that rainbow were effective predators on migrant fry, particularly on fry produced in stream channels. Trout were especially successful feeding on recently emerged fry, under conditions of low stream velocities, low turbidity, and on moonlighted nights. High light intensity, a short decreasing photoperiod, and handling or previous stress all increased sockeye survival. Ginetz (1972) observed that enhanced sockeye either formed loose schools, or did not school at all, and responded actively to predator stimuli; whereas experienced or handled (stressed) fry formed compact schools and were less active in response to predator stimuli.

Forester (1968) reviewed predation on sockeye fry in a number of locations; however, only in Six Mile Creek, Babine Lake, were rainbow trout present in large numbers. In this instance, trout were the major predator and consumed up to 65% of the newly emerged fry. Clearly, the potential for rainbow or steelhead predation on enhanced sockeye fry is high, particularly early in migration when the fry are naiverelative to predators. Predation on sockeye, in such circumstances probably is limited by the number of trout present and perhaps also by the presence of alternative prey (e.g. pink, chum, or coho fry).

Sockeye migrate to the sea in spring and early summer and are found in inshore areas in early June (Forester, 1968). Competitive interactions with migratory steelhead are probably limited by different feeding habits. Forester (1968) notes that sockeye feed on plankton and epibenthic invertebrates in coastal waters and occasionally take herring larvae in estuaries. Migrant sockeye are large (>20cm, Forester, 1968) and therefore predation on them by other smaller juvenile salmonids in estuarine and marine environments is unlikely.

Wild and enhanced sockeye are also preyed on by cutthroat trout. Again this predation occurs mostly during fry migrations but also occurs in lakes. Most of the sockeye are probably taken by adult cutthroat. Ricker (1941) reported in Cultus Lake that cutthroat between 300 and 399mm took sockeye slightly more frequently than those in the 200-299mm group. Both size groups took sockeye at all seasons; however, in May and early June cutthroat took larger numbers of sockeye fry than in other months. In April when the sockeye smolts moved into shallow waters before migrating seaward, predation by cutthroat again increased.

Dolly Varden and Arctic charr are often considered major predators on juvenile sockeye (Foerster, 1938; Semko, 1956; Thompson and Tufts, 1967; Thompson et al., 1971; Meacham, 1977); however, different charr stocks vary in their propensity to prey on salmon fry and there are many references reporting that salmon juveniles are insignificant in the diet of charr (DeLacy and Morton, 1943; Roos, 1959, Lagler and Wright, 1962; Armstrong, 1965). Where sockeye are consumed by Dolly Varden, the primary predators are fish between 150 and 300mm in length (Roos, 1959; Ricker, 1941).

Chum

During their short freshwater migration, in estuaries, and in their early marine rearing phase chum fry are preyed on by larger juvenile salmonids (Bakkala, 1970). In addition to coho and chinook smolts discussed previously, they are eaten by steelhead, cutthroat and Dolly Varden.

Although steelhead smolts prey on salmonid fry in both freshwater (Hunter, 1959) and estuaries (Loch, 1982), they are seldom numerous enough to influence chum stocks. No evidence contrary to this view was uncovered in the review.

Like coho smolts, resident and anadromous cutthroat trout have been considered major predators on chum fry (Pritchard, 1936; Hunter, 1959). They are, however, seldom as numerous as coho, Dolly Varden or sculpins and little quantitative data on the impact of cutthroat on chum populations was found.

Where cutthroat stocks are enhanced, they are often released at approximately the same time as enhanced chum fry. When these releases coincide severe chum losses have been observed (W. Foye DFO, pers. comm. Because chum fry seldom remain long in freshwater, such interactions are easily avoided by scheduling cutthroat releases about a week after any local chum releases.

Interactions in estuaries are less easily avoided, and although Levy and Levings (1978) noted that cutthroat did not prey on chum fry in the Squamish estuary, other authors (e.g. Armstrong 1971; Sumner 1972) reported that salmonid fry, in particular chum fry, were a major prey of cutthroat.

Pink

Predation during freshwater migration and early marine life has a major impact on pink salmon stocks; coho, chinook, steelhead, cutthroat and Dolly Varden are all recorded as predators on pink fry (Hunter 1959, Parker 1965, Pritchard 1936). Interactions between pink fry and a major predator, coho smolts, were discussed earlier as were pink fry losses to chinook. Emergence timing and the immediate outmigration of pink fry limits the probability of interaction between steelhead and pinks in freshwater to predation by older steelhead juveniles on pink fry. However, Hunter (1959) observed steelhead were one of the less efficient predators of migrating pinks. No documentation of steelhead predation on pink during estuarine or early marine life was located. In some areas of Alaska, Dolly Varden consume large number of pink fry (Dudiak, 1981), but in British Columbia their effects are not well documented.

Steelhead

In British Columbia most steelhead are released as smolts, although small numbers of fry are stocked in under-utilized freshwater areas.

Thus, like coho, enhanced steelhead can be involved in interspecific predatory interactions both as predators and as prey. Steelhead fry losses to other salmonids are not well documented and although wild steelhead smolts can be piscivorous (Fresh et al, 1981; Loch, 1982), they are usually reckoned to be too scarce to have a major impact on other salmonid species. Hatchery releases, however, are commonly concentrated and significant predation on other stocks under this condition remains a possibility.

Patten (1972) examined the stomachs of predators in two streams and a lake into which cultured sockeye, chum or chinooks were released. In Vance Creek, where chinook fry were released, rainbow trout were the more effective as predators than sculpins and coho, and the trout consumed an average of 9.88 chinook fry per trout. Given an appropriate size difference, steelhead smolts, particularly residual fish, can be expected to feed on wild and enhanced chinook fry.

Hunter (1959) indicated that steelhead were one of six main predators of chum and pink in Hooknose Creek, northern B.C., but that this species was a less effective predator on salmonid fry than other trout, salmon or sculpins. Upon emergence, chum fry migrate from their natal streams to the sea. Thus their time period in freshwater is minimal. Because steelhead emerge later in the year than chums, freshwater interactions between these species involve only predation by yearling or older steelhead on chum. Predation by residual and wild steelhead on chum fry in freshwater, therefore, can be expected to be limited in both time and degree. In estuarine and marine habitats, however, steelhead and chum are not only present at the same time but also the movements of the species through estuaries and offshore may be concurrent. Simenstad et al. (1982) noted that steelhead and cutthroat trout typically show a higher occurrence of juvenile salmonids in their diets than other estuarine predators such as cod, sculpins, and coho or chinook smolts. Estuarine and marine food studies (Patten, 1972; Fresh et al., 1981), however, have not documented steelhead predation on chum fry. Thus such predation is probably moderate.

Cutthroat

The extended freshwater residence typical of cutthroat trout results in large size and predatory interactions with other species. In freshwater, cutthroat prey on sockeye, pink and chum fry (Ricker, 1941; Hunter, 1959). In addition, they are known to prey heavily on other salmonids during their estuarine residence (Loch, 1982; Levy and Levings, 1978). Most of these interactions were discussed previously.

ENHANCEMENT OPERATION RECOMMENDATIONS

The preceeding species-by-species literature review suggests that there are a large number of interactions that are of potential concern to enhancement planners. Unfortunately, most of these interactions are poorly documented. Possible implications of these interactions, along with some recommendations for further study are outlined in the section following. There are, however, a few areas where species interactions are clear and where enhancement practises have evolved to ameliorate problem. Many of these practises are standard hatchery procedure, and these practises, along with some additional recommendations, are outlined in the following paragraphs.

COMPETITION

Competitive interactions between juvenile salmonids can result either in the disruption or displacement of one species by a behaviourally dominant species (Tripp and McCart, 1983; Bjornn, 1978), or in reduced growth and survival (Miller, 1958; Simenstad et al., 1980). Some species may only coexist at low densities, while in others, losses due to competitive interactions can be avoided.

Fry Releases

When juvenile salmonids are released as fry, a number of competition problems are possible:

Colonization

When coho, steelhead or stream-type chinook fry are released for rearing in freshwater, interactions with other species and with wild stocks of the same species are possible. The three main areas of concern are size, timing and habitat type. Solazzi et al. (1983) and Glova (1977) demonstrated the importance of size and timing in reducing the interaction between cultured and wild coho stocks. Where hatchery rearing time is minimized and outplants are made at the same time as natural emergence, hatchery fish are less likely to develop the aggressive, disruptive habits typical of fish reared at high density in hatcheries. Further, the cultured stock will not have reached the large size that apparently confers behavioural dominance. This approach, however may decrease the effectiveness of outplants, since the cultured stocks are likely to be at a slight disadvantage in the wild (Miller, 1958). As another example of the importance of release timing, Reimers (1963) suggested that hatchery trout are less hardy in the winter and he recommended releasing trout in the fall. If the objective is to maximize the survival of hatchery reared trout, this is probably a sound suggestion; however, if there is concern about wild stocks, early releases should aid in the preservation of wild stocks.

Where possible, outplantings should be made in habitats separated from other species or other stocks of the same species. Most evidence suggests that it is difficult to rear cutthroat trout in the same system as coho. Where both species are present as fry, cutthroat can be displaced by the larger coho fry and this may lead to local extinctions or to large reductions in the cutthroat population (de Leeuw pers. comm., Tripp and McCart, 1983). In areas where there are significant wild cutthroat populations, two ways to mitigate this problem show promise. Either coho stocking can be limited to low gradient areas that are avoided by cutthroat juveniles or, the system could be left fallow every few years to allow a cutthroat cohort to outgrow the coho competition. If coho are stocked in low gradient areas, care should be taken to ensure densities are not so high as to encourage upstream migration.

The agressive, schooling nature of cultured coho and other species may be related to rearing densities (Glova 1978b, Fenderson and Caprenter, 1971). The impact of colonization programs on wild stocks might therefore be decreased by rearing the fish to be outplanted at lower densities.

Migrant Fry Releases

Where pink and chum fry are released for seaward migration, or sockeye fry are released to migrate to a lake, the releases are usually made as large as possible to minimize the effects of predation. This, can result however, in local fry populations that exceed the carrying capacity of the receiving waters. This effect has been known for some time in sockeye (Foerster, 1944) In pinks and chum, however, the effect is less well documented. Simenstad et al. (1980) postulated that at high population levels chum and pinks may be forced to migrate away from estuarine and near-shore areas more rapidly than at low densities and thus reduce their growth and survival. Further work in this area is required before estuarine carrying capacities can be assessed with accuracy.

Stock Selection

Many aspects of salmonid morphology, behaviour and life-histories are inherited; however, the expresssion of such traits is not usually exclusively genetic. Instead, they are typically the result of genotype-environment interactions (for a review see Withler et al. 1982). This may make it possible to manipulate different gentic strains in combination with different rearing conditions to aleviate some interaction problems. For example, Roseneau (1984) demonstrated differences in the inherited levels of aggresssion in different coho stocks. Thus, in outplants, if copmetitive interactions are a potential problem, stocking a low - aggresssion strain may reduce the problem. Similarly, the manipulation of downstream migration times may reduce some classes of interaction. Murray (1980) suggested that interpopulation variation in egg development rates and thus emergance times, are partially inherited. Thus, for example, appropriate strains of chum salmon might be used in enhancement projects to shift downstream migration timing to a period which did not coicide with a smolt migration. Clearly, the use of different genetic strains to reduce aggression or shift migration times needs more consideration, however, stock selection shows enough promise as a technique for reducing negative interactions to warrant further investigation.

Smolt Releases

Most of the information on smolts uncovered during this review concerned predation. Although all of the points made above are to some extent true for smolts, smolt numbers rarely are large enough to result in competitive interactions. In addition, hatchery released smolts usually move out of fresh water and into estuarine or marine areas rapidly. Thus, their activities are poorly documented. In cutthroat and steelhead trout, however, some hatchery smolts may revert to parr and remain in freshwater. These residuals will often be larger and may out compete wild parr (Slaney and Harrower, 1981). In these instances, size grading and releases into the lower reaches of streams are recommended. Grade-downs appear to have a higher incidence of residualism (Tipping, 1982) than larger fish and should either be destroyed or stocked in isolated lakes where they will not disrupt wild stocks.

PREDATION

Juvenile salmonids from enhancement facilities are potentially both predator and prey relative to other stocks or species. On one hand, pink and chum may suffer massive mortalities from predation during their freshwater migrations; whereas coho and steelhead gradually shift during their freshwater residence gradually shift from prey to predators. Thus, there are two main problems:

a. reducing predation on hatchery fry releases.

b. minimizing the impacts of smolts on both wild stocks and other hatchery stocks.

Fry releases

All salmonid species are, to some extent, piscivorous (Ricker, 1941; Rounsefell, 1958, Hunter, 1959; Roos, 1959) and predation in fishes is typically size related. Thus, when their life histories overlap small fish such as pink and chum fry will be preyed on by other larger salmonids. There are however some factors that can effect the magnitude of these losses.

a. Fry are particularly vulnerable when released in areas where predators are aggregated. Release locations such as small bays, heads of inlets, river mouths or dams can force fry to run gauntlets of predators and thus increase the likelihood of significant losses.

b. Predator-prey in relationships salmonids typically are size related and large predators usually take more and larger prey (Bams, 1967: Taylor and McPhail, 1984). Thus, where the size difference between predators and fry can be minimized, survival will probably increase.

c. Fry condition, both at release and during migration, can have an impact on survival. Thus hatchery handling, disease, and parasites affect fry survival (Wedemeyer, 1980). Ginetz (1972), however, suggests that handling sockeye fry results in better schooling and predator avoidance. In addition, where fry are disoriented by movement over dams, through tailraces, or through extreme temperature or chemical changes, losses will increase (Brown and Moyle, 1981).

d. Except where fry numbers far exceed predator numbers, variation in the predator/prey ratio or increases in predator numbers may result in increased fry losses (Petermann and Gatto, 1978). Predator responses to increased prey are not well understood, however, where predators are able to aggregate prior to releases or during migrations, losses will be much greater. Predator buildups are aggrevated when small numbers of fry are permitted to escape prior a major release (Hadley, 1979).

Fresh et al. (1980) examined the effects of various enhancement techniques on freshwater survival of chum salmon and reported that survival can be increased by manipulating fry releases.

a. In order to avoid visual predators fry should be released at night or during periods of high water turidity or increased velocity (Fresh et al., 1980; Ginetz and Larkin, 1976).

b. To swamp predator responses, fry should be released in larger numbers. There is some question (Peterman and Gatto, 1978) as to how large a release is required to accomplish swamping.

c. To reduce the distance fry have to travel and thus the duration of exposure, fry should be released as close to estuaries or rearing areas as possible.

Mace (1983) suggested that predation on chinook fry could be alleviated by releasing fry in the late evening, close to the estuary and at high tide such that fry were forced out of the river and offshore.

Smolt Releases

Where smolts, or fry that will rear to smolt stage in freshwater, are released the likelihood predation problems are greater. Whereas fry outplants suffer losses in the manner described above, coho, chinook, steelhead and cutthroat smolts prey on other salmonid species. Therefore, in addition to the inverse side of all of the points made above, losses due to smolt releases can be minimized by the following:

Timing

When the temporal overlap between species is reduced predation losses are also reduced. For example, when chum or pink fry are clear of a system before coho smolts are released the extent of predation from that source is reduced (Aimes, in prep; Westcott, et al., 1983).

Duration of Freshwater and Estuarine Rearing

Long freshwater residence times are associated with increased predation. In areas where this becomes a problem it has been observed that larger, or later smolts, spend less time in fresh and estuarine waters before moving offshore than smaller or earlier smolts. Thus, larger smolts are in contact with, and can prey upon, freshwater and inshore prey species for a lesser time (Westcott, et al., 1983; C. Levings, DFO pers comm, Myers, 1980).

Residualism

When the time spent in freshwater by smolts or presmolts is extended, the opportunities for predation are enlarged. This problem is especially acute in steelhead and cutthroat trout. In these species, fish may remain in freshwater for their entire lives rather than migrate to sea. As noted earlier, such residuals typically revert to parr and take up stream residence. Thus, they constitute a loss to the fishery and remain a constant threat to fry (Slaney, 1981; Tipping, 1982). As the proportion of nonmigrating fish appears inversely related to size, it may be that "grade downs" should be used to stock isolated lakes and streams where residuals are not likely to interact with other stocks. Slaney and Harrower (1981) recommend releasing steelhead smolts only in the lower reaches of streams, thus limiting the effects of residualism.

RECOMMENDATIONS FOR FURTHER STUDY

To identify detrimental interactions and mitigate against their effects, enhancement programs should incorporate a number of basic studies into the planning process. These studies fall into five categories which are progressively more specific in their goals.

Baseline Studies

Baseline bio-reconnaissance studies similar to those currently conducted for major facilities developments should be undertaken before all enhancement programs or expansions. So that the disruption of existing salmonid stocks can be evaluated and minimized. Site specific information rather than general standards, should be used to plan for the introduction of new stocks.

Statistical Analyses

Statistical analyses have suggested interaction effects in several cases. For example, Aimes (in prep) used correlation to indicate coho-pink interactions in Port Susan, Washington, and Westcott et al. (1983) at Big Qualicum Hatchery used regression to suggest the impact of coho on chum at Big Qualicum. Where data are available, such analyses should be conducted as a preliminary planning step. The collection of time series data on associated stocks and species should be part of the evaluation process for all major enhancement projects.

Interspecific and Intraspecific Experimental Studies

Where "exotic" stocks or species are to be introduced, experimental and field studies on allopatric and sympatric populations should be used to assist in the prediction of impacts. For example, coho introductions in the upper Fraser River will probably influence chinook stocks, and information on the interactions between coho and interior, rather than coastal, chinook juveniles will be required to evaluate their problem. Similarly, headwater planting of steelhead fry will probably have impacts on cutthroat and other resident species.

Enhancement Monitoring Programs

One reason for the absence of data on interactions involving juveniles released from enhancement facilities is that, although local personnel usually empirically adapt their releases to suit local conditions, there is little opportunity or incentive for reporting such observations. Thus, each facility starts anew or with only modest assistance from other experiences.

To detect and avert potentially deleterious interactions with minimum losses, release monitoring programs should be conducted with the aid and input of local facility personnel sor several release cycles. Some of the paramenters that could be examined include:

- stomach contents of the released stock, wild stocks and potential procedures.
- growth rates
- visible interactions

In addition, other stocks (espcially wild stocks) in the immediate area of a new facility should be monitored for several release cycles. In Washington simple correlations of size of stocks have been instrumental in detecting negative interactions.

Experimental Work

Some of the interactions that are potentially important to the success of enhancement operations are poorly documented. Therefore detailed examinations of interactions in a number of areas is therfore recommended.

- Chinook and coho stockings in interior areas are increasingly common. Therefore, a study of microhabitat use and interactions in interior habitats would be valuable. The wide variations in chinook, and to a lesser extent coho life histories, suggests that there may be substantial differences in the interior from the habitat partitioning noted in coastal stocks. This is particulalry important in the upper Fraser where there are many wild chinook stocks but no natural coho populations.

- How to estimate the rearing capacity of estuaries has been a subject of speculation for some time. As more enhancement facilities producing pink and chum come on line, the potential for habitat overloading and thus interactions amoung species and between wild and cultured stocks increases. Although work of this type is underway in Puget Sound, and to a lesser extent in B.C., further exploration, particularly in the coastal inlets of B.C. may be worthwile.

- Habitat and resource partitioning observed by Healey (1979, 1980) and Levy et al. (1979) suggests that there may be some interaction between chinook and chum salmon on estuaries. As this could have an impact on estuarine carrying capacity and juvenile success, further study is recsommended.

- Healey (1984) has noted that there may be a genetic basis for the life history differences between 'stream type' and 'ocean type' chinook salmon. As stream residence is also related to density, stocking cultured chinook fry into streams may result in changes in the relative success of the two types. The implications of stocking under these conditions, and the best approaches to this problem also warrant further examination.

SUMMARY

The available literature and information on interactions among cultured and wild stocks of juvenile salmonids were reviewed. The intention was to review and document existing knowledge on competition, predation and other interactions among enhanced stocks, and between enhanced and wild stocks of Pacific salmon, steelhead and cutthroat trout. The objective of the review was to identify and assess areas of concern in the planning and development of enhancement strategies. Information was gathered through manual and computer literature searches and interviews with research and technical personnel working in the area of juvenile salmonid production. In addition, letters were sent to institutions that sponsor research on salmonids. Where possible, the review emphasized research published in primary journals. Such reports are subject to external review, and the data and interpretations tend to be more rigorous than those found in the "grey" literature.

Unfortunately, primary journal articles in this subject area are rare and most of the data comes from government and agency technical reports, as well as personal communications with people working in the field.

TABLE 2
Summary of interactions involving enhanced juvenile salmonids

Life History Stage	Interacting Salmonid Species						
	Coho	Chnk	Chum	Pink	Sock	Stl	Ctt
A. Coho							
Freshwater	--	-	+++	+++	++	--	--
Estuarine	-	x	+++	+++	x	x	x
Early Marine	x	x	+++	+++	x	x	x
B. Chinook							
Freshwater	-	-	x	x	x	±±	±
Estuarine	x	x	?	?	x	?	x
Early Marine	x	x	x	x	x	**	x
C. Chum							
Freshwater	***	x	x	x	x	*	**
Estuarine	***	x	--	--	x	?	x
Early Marine	***	*	--	--	?	?	x
D. Pink							
Freshwater	***	x	x	x	x	*	**
Estuarine	***	?	--	--	x	x	?
Early Marine	***	x	--	--	?	x	x
E. Sockeye							
Freshwater	**	x	x	x	--	**	**
Estuarine	x	x	x	x	x	x	x
Early Marine	x	x	x	?	x	x	x
F. Steelhead							
Freshwater	±	±±	++	++	++	--	--
Estuarine	x	?	?	?	x	?	x
Early Marine	x	+	?	?	-	?	x
G. Cutthroat							
Freshwater	±±±	±±	++	++	++	--	---
Estuarine	x	?	x	?	x	x	x
Early Marine	x	x	x	x	x	x	x

Types and Degrees of Interaction

A. Documented	Slight	Moderate	Strong
Predator	+	++	+++
Competitor	-	--	---
Pred & Competitor	±	±±	±±±
Prey	*	**	***
B. Undocumented			
Likely	?		
Unlikely	x		

Where data on enhanced stocks of a species were lacking, observations on wild stocks were reviewed, and the probable effects of enhancement inferred.

Coho releases appear to pose the most serious set of problems. Coho smolts can prey heavily on other juvenile salmonids (Table 2) and care must be taken to separate (in time or space) coho releases from those of other species, particularly chum and pink. Coho fry outplants require similar care. Hatchery coho fry are typically larger and more aggressive than wild fry. Thus outplants may result in the displacement of either wild coho or other species.

Variability in chinook life history patterns make assessment of interactions involving this species difficult. Although there are scatter references to predation on other salmonid fry by chinook smolts, the major problems with this species appear to concern competitive interactions among fry. Intraspecific, density-dependant competition is reported for both wild and cultured juveniles. In addition, overlaps in migration timing, food, and the use of space suggest there is the potential for competition in freshwater between chinook and steelhead and in estuaries between chinook and chum.

Little direct information was found on interactions involving juvenile sockeye from enhancement facilities. Since most of the facilities in British Columbia are spawning channels that release fry directly into lakes, such interactions probably are similar to those of wild stocks. Thus predation during lake residence as well as during fry and smolt migrations may be important. At these times sockeye fry are preyed on by yearling coho, resident and juvenile rainbow trout, cutthroat trout and charr.

Chum fry are particularly vulnerable to predation by coho, steelhead and cutthroat trout smolts. Losses due to predation can be reduced by scheduling chum releases before smolt migrations; releasing fry at night; releasing large numbers of fry at one time; and locating releases in areas where the fry can disperse easily. In addition, the fry should be large and in good condition. The growth and success of chum fry may also be influenced by competition with other chum stocks, pink fry, and possibly also with chinook migrants.

Pink fry also are subject to predation by coho, steelhead and cutthroat trout smolts and losses may be larger than those of outmigrant chum fry. Measures similar to those recommended for chum salmon should help to minimize these losses. Competition between chum and pink fry may have deleterious impacts on pink growth and survival.

Under some conditions steelhead trout fry may compete for space with stream-rearing coho and chinook fry . Usually, however, steelhead are segregated from coho and only interact with chinook when the fry are of similar size. Yearling and older steelhead juveniles also prey on pink, chum and sockeye fry. Steelhead smolts, however are seldom numerous enough to have an impact on the success of other stocks. Cultured steelhead, however, can have negative impacts on wild populations. If released hatchery fry are larger than wild fry they can dominate and thus displace wild fish. Some hatchery released steelhead smolts revert to parr, and these remain in the stream and compete with wild stocks for food and space.

Young of the year cutthroat trout appear to be especially vulnerable to disruption and displacement by coho or steelhead fry stocked in the same habitats. Where cutthroat stocks are to be enhanced, or preserved, it appears necessary to exclude the other species or at least to limit them to lower gradient areas that are less favoured by the cutthroat young. Cutthroat smolts can prey on coho, chinook, sockeye, chum and pink fry. Thus releases of cutthroat smolts should not be scheduled until these species have migrated out of the system. In addition, cutthroat smolts like steelhead, are subject to residualism. This can result in lost production in other stream rearing stocks through increased predation and competition.

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- D. Chuddick
- A. de Leeuw
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