

AN INVESTIGATION OF A POTENTIAL CARRYING CAPACITY OF COHO AND CHINOOK  
SALMON IN THE GEORGIA STRAIT

by

SCOT ALEXANDER MOUNTAIN

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Department of Zoology

The University of British Columbia  
Vancouver, Canada

Date May 2nd, 1997

## ABSTRACT

Stable or decreasing catches in conjunction with increasing hatchery releases have suggested decreasing marine survival rates for populations of Pacific salmon (*Oncorhynchus sp.*) in the Georgia Strait. I examined the possibility that a carrying capacity is imposing limits on the populations of coho (*Oncorhynchus kisutch*) and chinook (*Oncorhynchus tshawytscha*) salmon. Two investigations were carried out; the first involved an examination of the impact that juvenile salmon have on their food supply. The second used a computer model to predict the possible results that a hatchery based fisheries manipulation might produce under different experimental protocols.

The feeding study suggested that juvenile salmon might be having a much greater impact on their available food supply than has previously been suspected. Overall, it was estimated that chinook and coho together consume an average of 4% to 6% of their main foods daily. If these impacts are taken together with those of other species, this suggests that a carrying capacity might well be important.

A hatchery manipulation experiment is one obvious way to test for a marine survival limit as implied by a carrying capacity. Using a metagaming approach to model such an experiment, insights were obtained into how it could be performed most efficiently. The results suggest that, depending on the required outcome, it would be advisable to maintain current exploitation rates of both coho and chinook stocks during such an experiment. Other factors that would favor a rapid conclusion to the experiment are extreme as opposed to conservative manipulations, and minimal attempts to rebuild stocks through other means. However, even if these recommendations are heeded, the model suggests that a hatchery experiment might need to be a long term project. With reductions in hatchery releases as high as 75% every second year, average times to produce conclusive results were on the order of a decade or more.

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## CHAPTER 1: GENERAL INTRODUCTION

The coho (*Oncorhynchus kisutch*) and chinook (*Oncorhynchus tshawytscha*) fisheries in the Georgia Strait are among Canada's most economically important natural resources. From 1987 to 1990, the commercial catch of these two species generated an average of \$63 million per year (DFO 1992 a). However, this figure pales in comparison to the income generated by tourism related to the extensive sport fisheries based in the Georgia Strait.

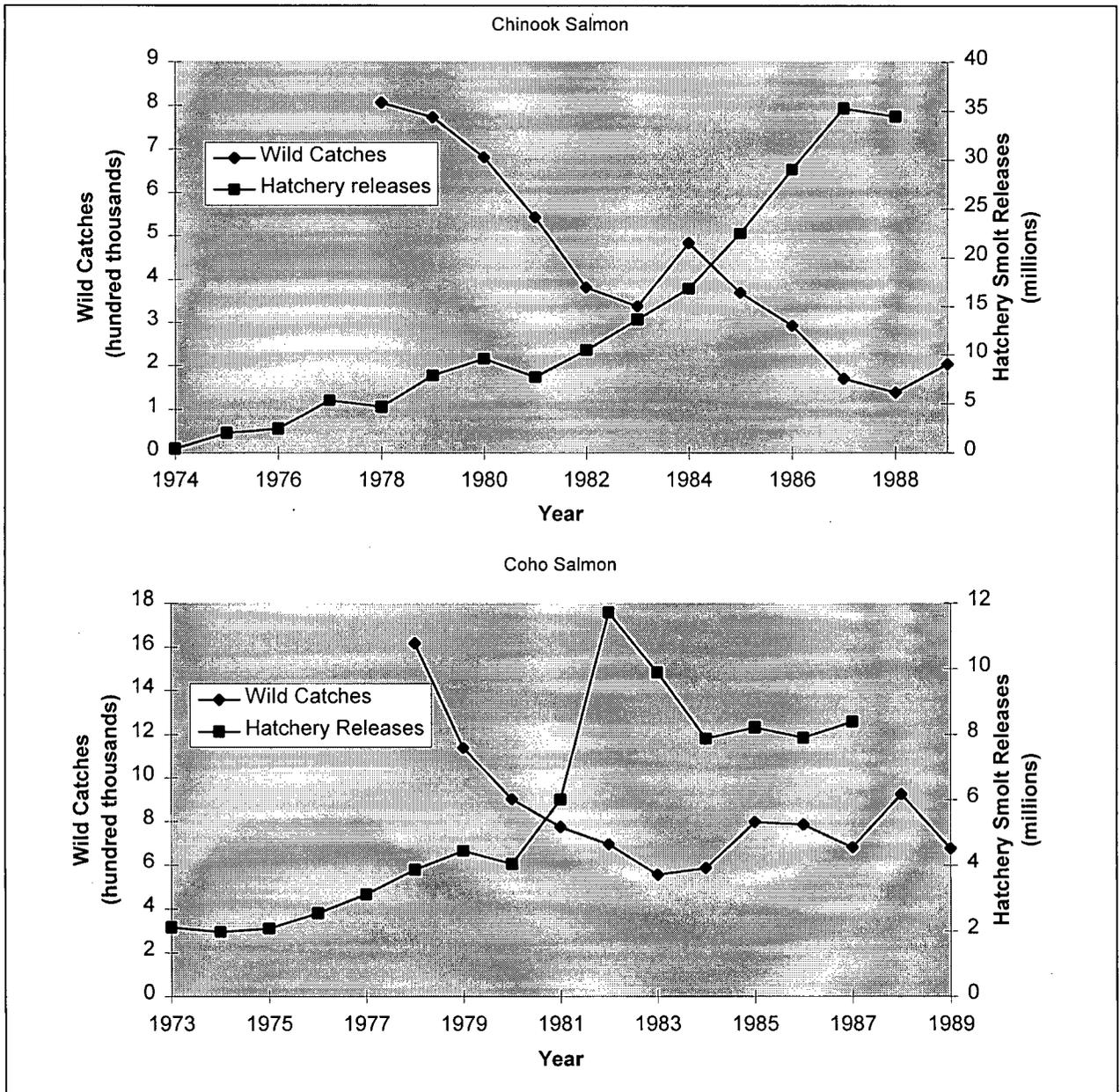
Historically, recruitment to these fisheries came primarily from wild fish that spawned in the streams and rivers around the Strait. However, in the early 1970's hatcheries supported by the Canadian Salmonid Enhancement Program began to contribute a significant proportion of fish to the total catch. Since then, the proportion of hatchery fish in Georgia Strait catches has been steadily increasing, while the wild fish proportion has been declining. By 1992, hatchery fish constituted up to 20% of the chinook catch (Cross et al. 1991), and half of the total coho catch (Walters 1993).

The increase in hatchery releases and catches has not been accompanied by a proportional increase in the total numbers of fish caught in the Strait. In the case of coho, overall catches have remained more or less constant over the last thirty years (Walters 1993). However, proportions of wild fish in the catch are significantly lower than historical levels. Georgia Strait chinook catches have shown a significant decline from 1978 to 1989 (Cross et al. 1991). This decline in total catches is mirrored almost exactly by the decline in numbers of wild fish being caught. Figure 1 illustrates the increasing hatchery releases, and the concurrent decreasing wild catches of both species.

The stable or decreasing catches, in conjunction with increasing hatchery releases into the Strait, suggests a major negative impact on the productivity of wild salmon stocks. Concern among British Columbia's fisheries managers and scientists has led to several investigations of possible causes of the wild stock decline. Initial

recommendations from the Department of Fisheries and Oceans (DFO) for reversing the trend focussed on fishing restrictions, habitat restoration, and continued hatchery production to enhance the failing stocks (DFO 1992 b).

Figure 1. Decreasing catches of wild coho and chinook in conjunction with increasing releases from hatchery operations have occurred in the Georgia Strait. Data from Cross et al. 1991.



More recently, it has been suggested that the combination of increasing hatchery releases with stable or reduced returns may in fact suggest the existence of a carrying capacity limit that imposes an upper threshold on the numbers of salmon the Strait can produce. Thus, it may be that the decline in wild stocks is a result of competition with hatchery fish for limited resources. Other attempts to explain the decline have concentrated on environmental conditions such as ocean temperatures and pollution.

In total, four main hypotheses have been advanced to explain the declines in wild coho and chinook abundances (Walters, 1993). These hypotheses are;

1. Over fishing.
2. Freshwater rearing habitat limitation.
3. Changing oceanographic conditions.
4. Marine carrying capacity.

Each of these explanations has plausible arguments for and against it.

The overfishing hypothesis is one that is commonly touted by both the media and DFO. In fact, there is supporting evidence to suggest that a very low proportion of wild fish that recruit to the fishery survives to spawn. However, serving as evidence against this hypothesis is the lack of information relating spawning stock sizes to recruitment. In fact, there are indications that some salmon fisheries have survived under much higher exploitation rates. For example, Fraser River sockeye have been shown to sustain and even increase their populations under fishing impacts that are similar to those experienced by coho and chinook in the Georgia Strait (Walters 1993).

Another popular theory is that the decline in wild stocks is the result of a loss of rearing habitat in freshwater streams and rivers. There are certainly some major impacts on these habitats due to human activities such as forestry, urban development and mining. However, it is not clear whether these activities impact rearing habitat positively, negatively or not at all from the fish's point of view. In fact, evidence exists that habitat disturbances caused by logging operations may actually be associated with increased smolt production (Holtby

1988). Even if habitat impacts are negatively affecting smolt production, it is highly unlikely that the amount of habitat destruction that has occurred could account for the large reductions in wild abundance (Walters 1993).

Further evidence against the overfishing and habitat destruction hypotheses is given by the apparently reduced marine survival rates observed for salmon in the Georgia Strait. These estimates come from coded wire tag (CWT) data summarized by Cross et al. (1991). This suggestion of reduced survival implies that the smolt numbers entering the Strait must have stayed the same, or even increased, in order to produce the observed catches. However, this would not be the case if overfishing or habitat limitation was occurring. If either of these hypotheses were correct, then smolt production must have declined, and marine survival must have remained constant or even increased. Unfortunately, the reliability of the marine survival estimates is questionable, especially for wild stocks. Thus, they cannot be taken as definitive evidence against the overfishing or habitat limitation hypotheses.

CWT data also provide evidence that any limit on salmon survival is impacting the young fish, in their first year at sea. This conclusion can be drawn from the fact that the proportion of wild one year old "jacks" in the catches has not decreased relative to the older fish (Cross et al 1991). Therefore, there does not appear to have been any reduction in survival between one year of age and later years. This means that whatever is reducing survival rates is probably acting on the smolts shortly after they go to sea.

The two hypotheses that are most consistent with decreased marine survival in the Strait are poor oceanographic conditions, and a marine carrying capacity limit. It is impossible, with the historical data, to either prove or disprove that an oceanographic influence has caused the decline in salmon survival. Environmental conditions such as water temperature and salinity are constantly changing, and these changes undoubtedly impact the resident species both positively and negatively. In particular, sea surface water temperatures have increased somewhat since the late seventies, and subsequent El Ninos have been responsible for higher than normal temperatures in the early 1990s. However, because of the complexity of the interactions in the Strait in response to changing environmental conditions, it is not an enlightening exercise to hypothesize how these conditions might negatively impact salmon survival.

The hypothesis that appears to best fit the observations is that of a marine carrying capacity limit. This hypothesis claims that, due to limited available resources, a restricted number of salmon can be reared in the Strait each year. Thus, the proportion of wild salmon in the total stock is being reduced as more hatchery fish claim a share of the limited total capacity for adult production. The most obvious factor that might impose such a restriction is the limited availability of food resources. Given that the annual productivity in the Strait must be finite, it is plausible that the Strait can only produce a circumscribed number of individuals of each resident species.

There is another reason that the possibility of a carrying capacity limit in the Strait should be investigated. Of the four possible hypotheses defining the situation in the Strait, a carrying capacity limitation would be the most easily corrected by fisheries managers. A simple reduction in hatchery outputs to appropriate levels should be enough to improve the survival of wild stocks in the Strait. Therefore, it is important to analyze the Georgia Strait fisheries for any evidence that the hatchery program may be the direct cause of the destruction of wild salmon stocks.

The focus of my study was two-fold. Initially, I attempted to investigate the food supply of Georgia Strait smolts to see whether or not food could be imposing a carrying capacity limit on production. The second part of my project involved using a computer model to help design a hatchery based experiment that could aid fisheries managers in differentiating which of the four hypotheses is governing the current situation in the Georgia Strait. The concept of this experiment is to directly manipulate total hatchery smolt production on a large scale, to determine whether marine survival rates respond positively to hatchery smolt reductions as predicted by the carrying capacity hypothesis.

## **CHAPTER 2:**

### **A DIRECT INVESTIGATION OF FOOD SUPPLY**

#### **2.1. INTRODUCTION**

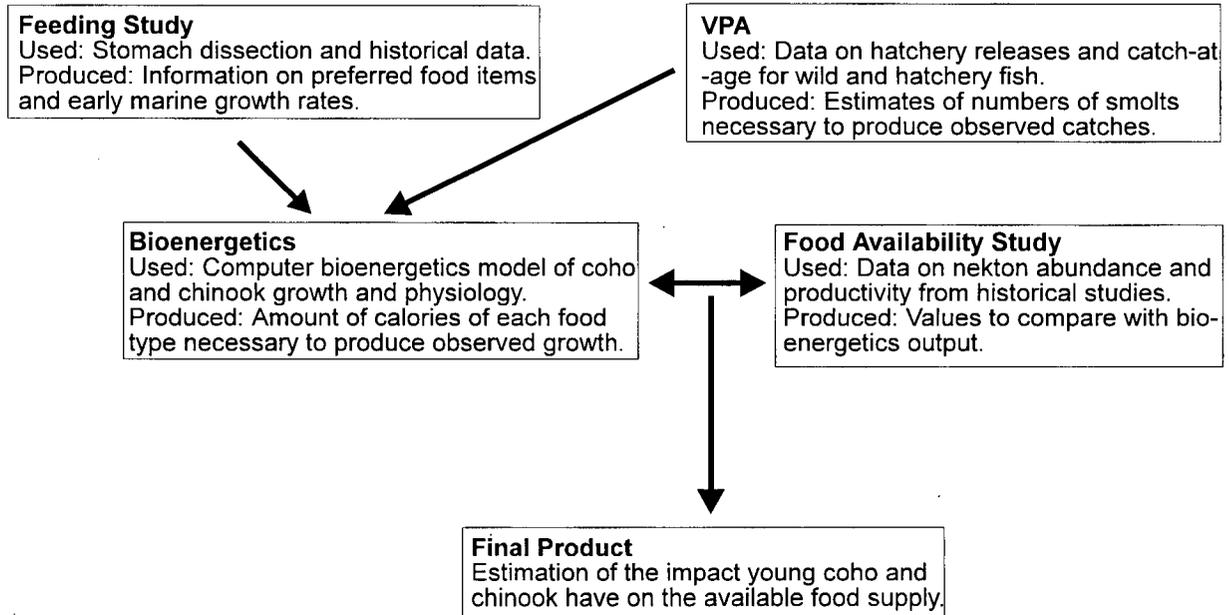
This chapter details my attempt to determine whether or not there is evidence of a food limited carrying capacity for coho and chinook smolts in the Georgia Strait. The investigation proceeded via five steps (Figure 2). The first step was a detailed analysis of the main food items being taken by smolts in the Georgia Strait. The stomach contents of nearly 600 smolts were excised and identified in order to determine what prey were preferred.

Upon completion of the feeding study, a modified Virtual Population Analysis was performed, using existing catch statistics for Georgia Strait fisheries. This analysis provided an estimation of the total numbers of fish of various sizes present in the Strait over time.

Having obtained detailed information on what the smolts were eating, and how many of them were present, a bioenergetics model was used to combine this information with smolt growth data. This model provided an estimation of the total food consumption needed to produce the coho and chinook populations in the Georgia Strait. These food requirements were apportioned out to specific food items in appropriate proportions as indicated by the feeding study.

The final step was to compare the estimates of the amount of major food items being consumed with estimates of food availability. Due to a lack of directly relevant food availability data, abundance and production estimates for the major prey items were obtained from historical oceanographic studies of the Georgia Strait and nearby coastal environments. This step was the constraining factor in my ability to draw firm conclusions about the carrying capacity in the Strait. Because of this difficulty, the results of the feeding study may best be used to guide further research. Nevertheless, the final result of this procedure was a comparison of the amount of food being eaten by coho and chinook with the amount of food apparently available to them. This comparison was examined to ascertain whether or not it suggested the existence of a carrying capacity limit.

Figure 2. Flow chart showing the procedures involved in the direct investigation of the food supply. Results of the feeding study and VPA were used in the bioenergetics model. Bioenergetics results were compared with abundance estimates to produce an estimate of overall exploitation.



## 2.2. FEEDING STUDY

This section describes the stomach content analysis of the salmon smolts. This procedure was carried out in order to gain a better understanding of the food items that are important to young coho and chinook in the marine environment. It was necessary to obtain this information in order to allow a comparison of the foods the salmon were eating with the available amounts.

### 2.2.1. Materials and Methods

In the summer of 1993, juvenile coho and chinook salmon were collected in conjunction with the Georgia Strait Juvenile Salmon Survey being carried out by the Pacific Biological Station in Nanaimo, B.C. Fish were sampled from four separate cruises, on May 25 through 28, June 14 through 17, June 22 through July 9 and July 5 through 8. Three of the cruises followed a preset series of transects that crossed the strait, and extended from the Fraser River plume (123° 23' W latitude, 49° 2' N longitude) in the south to Qualicum Bay (124° 37' W latitude, 49

° 26' N longitude) on the northern end (Figure 3). Fishing on the fourth cruise was concentrated in the area of the Fraser River plume.

Sets were generally from 30 to 60 minutes in length, with the shorter time interval being used when the nets were filling more quickly. Most of the sets occurred during daylight hours. 25 of the sets on the Fraser River Plume Cruise occurred at night.

Fish were caught from the charter fishing vessel Qualicum Producer, using a dual beam trawl design. Two nets, each with a mouth opening of approximately nine metres circumference, were trailed from outriggers located amidships. The nets were trailed off the stern, well clear of the wake of the vessel. Sampling extended from the surface to a depth of 6 to 7.5 metres. Mesh size on the cod end of the nets was 2.5 centimetres. A liner with a mesh size of 1.5 centimetres was used in the nets.

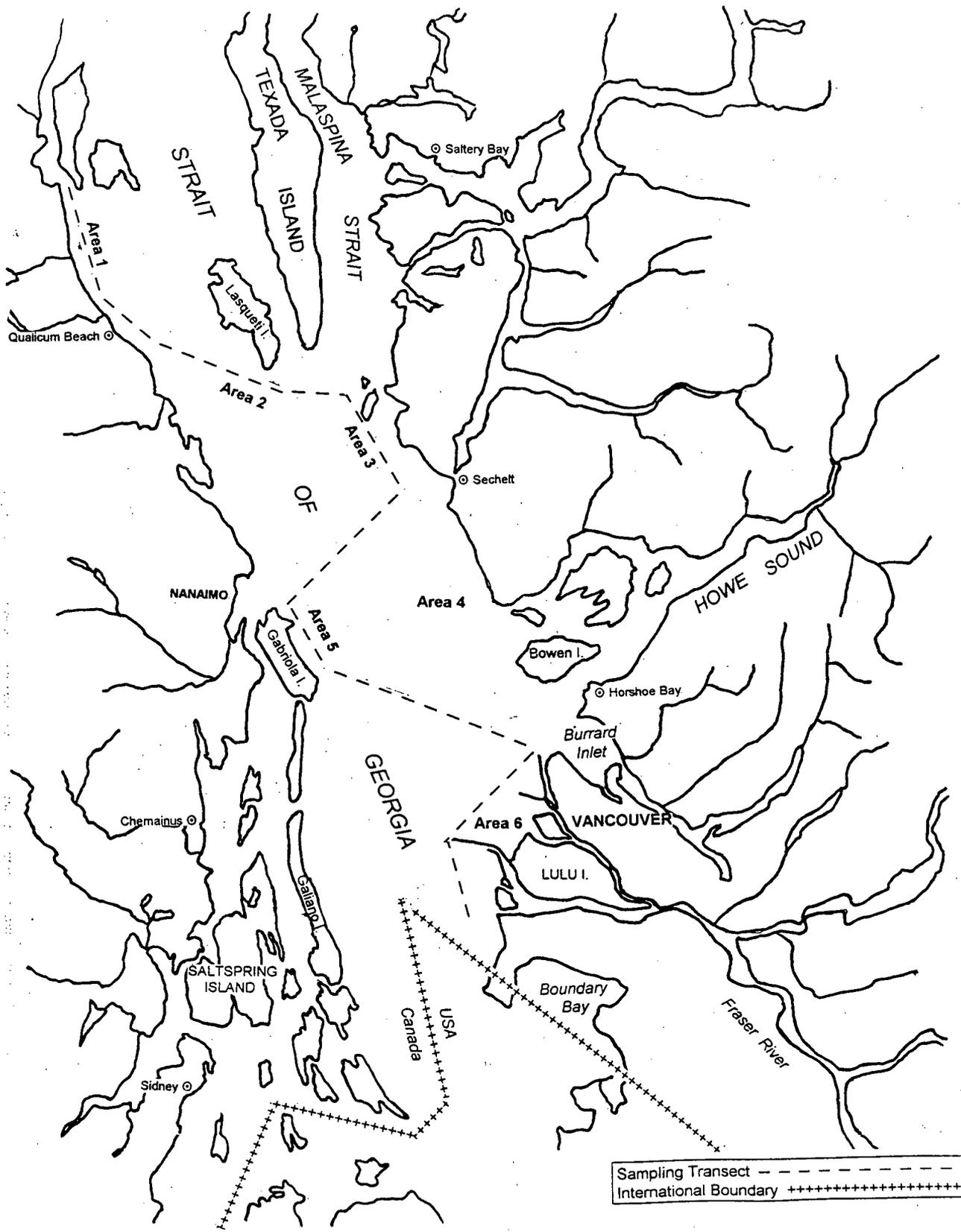
Salmon were rapidly sorted from the catch and identified as to species. They were then measured, and either frozen or stored in 10% formalin for later analysis in the lab.

### **Subsampling**

The first three cruises, which covered the entire strait, were divided geographically into six main areas depending on their depth and proximity to land (Figure 3). For every cruise, up to 30 fish of both species were randomly sampled from the catch from each area. If fewer than 30 of a species were caught in an area, then all of that species from that area were analyzed. For example, if, during cruise one, 75 chinook were caught in area three, then 30 were randomly selected to have their stomachs excised. If only 12 coho were caught in the same area, all of their stomachs were analyzed.

For the Fraser River Plume cruise, chinook were randomly drawn from a total of 84 separate sets. Since only 21 coho were caught on the entire cruise, all of their stomach contents were analyzed.

*Figure 3. Location of the stomach sampling cruises on the Georgia Strait. Three of the cruises followed the transects shown. These were further subdivided into areas as shown. The fourth cruise concentrated on the Fraser River plume.*



Sampling Transect - - - - -  
 International Boundary + + + + +

Stomachs were excised from preserved fish in Nanaimo, and stored in 10% formalin for transportation back to Vancouver. Once in the Vancouver lab, stomachs were blotted dry and weighed on an electronic balance to the nearest  $1 \times 10^{-5}$  grams. Stomachs were then dissected, and the contents were emptied, rinsed, and examined under a dissecting microscope. The contents were identified and sorted into taxonomic categories. After being sorted into taxonomic groupings, the items in each group were blotted dry and weighed separately. The empty stomachs were also blotted and weighed.

In total, stomachs from 575 juvenile salmon were analyzed. Of these, 335 were chinook and 240 were coho.

After the stomach contents of each fish were quantified individually, fish were pooled into five groupings. Each group consisted of fish that had been caught within four day (ninety-six hour) time periods. This allowed a temporal comparison of their diet compositions over the summer.

### 2.2.2. Results

For each time period, the average frequency of occurrence and the average numerical abundance by weight of each prey item was calculated (Tables 1 and 2).

*Table 1. Frequency of occurrence and abundance by weight of chinook stomach contents for five sampling periods during the summer of 1993. Italics show sample size.*

Prey	May 25-28 (109)		June 13-16 (93)		June 21-24 (41)		June 26-29 (28)		July 4-7 (54)	
	FO (%)*	AW (%)*	FO (%)	AW (%)	FO (%)	AW (%)	FO (%)	AW (%)	FO (%)	AW (%)
Fish larvae	22.9	12.6	26.9	12.5	48.8	17.4	32.1	13.3	33.3	14.0
Digested matter	38.5	23.1	72.0	25.6	97.6	42.9	82.1	33.2	75.9	41.1
Insecta	78.0	59.4	38.7	11.1	46.3	5.7	42.9	12.4	33.3	19.3
Gammaridean Amphipods	21.1	1.4	18.3	3.7	2.4	0.4	0.0	0.0	3.7	0.3
Hyperidean Amphipods	0.0	0.0	5.4	0.1	4.9	0.0	7.1	0.4	9.3	0.6
Cancer sp. larvae	27.5	1.6	40.9	12.8	65.9	28.6	64.3	21.6	55.6	23.6
Porcellanid larvae	0.9	0.9	40.9	33.3	4.9	2.2	50.0	19.1	1.9	0.6
Euphausiacea	1.8	0.1	3.2	0.9	0.0	0.0	0.0	0.0	1.9	0.2
Other identifiable matter	14.7	0.1	23.7	0.1	26.8	2.9	7.1	0.0	27.8	0.2

\* Frequency of occurrence (FO) indicates the number of nonempty stomachs in which the prey item was present in any amount. Abundance by weight (AW) indicates the percent of the total weight of stomach contents constituted by the prey item.

Any prey item that consistently made up more than 5% of the diet (by weight) was considered to be a major prey item. These included fish larvae, terrestrial insects and cancer sp. larvae for coho, and the same items, with the addition of porcellanid crab larvae, for chinook. The average percent abundance by weight was plotted for each of these items for each species (Figures 4 and 5).

*Table 2. Frequency of occurrence and abundance by weight of coho stomach contents for five sampling periods during the summer of 1993. Italics indicate sample size.*

Prey	May 24-27 (89)		June 13-16 (71)		June 21-24 (11)		June 26-29 (8)		July 4-7 (51)	
	FO (%)*	AW (%)*	FO (%)	AW (%)	FO (%)	AW (%)	FO (%)	AW (%)	FO (%)	AW (%)
Fish larvae	50.6	21.4	40.8	11.2	63.6	16.8	62.5	22.5	21.6	5.2
Digested matter	82.0	33.2	81.7	27.5	81.8	18.6	75.0	18.4	80.4	18.3
Insecta	92.1	34.8	39.4	10.8	72.7	10.3	0.0	0.0	5.9	0.3
Gammaridean Amphipods	49.4	4.3	5.6	0.1	9.1	1.3	0.0	0.0	2.0	0.0
Hyperidean Amphipods	1.1	0.1	19.7	2.2	18.2	2.2	0.0	0.0	17.6	1.9
Cancer sp. larvae	65.2	5.7	74.6	45.8	81.8	50.9	87.5	59.1	94.1	74.1
Porcellanid larvae	0.0	0.0	4.2	0.8	0.0	0.0	25.0	0.0	3.9	0.0
Euphausiacea	0.0	0.0	5.6	1.3	0.0	0.0	0.0	0.0	0.0	0.0
Other identifiable matter	15.7	0.6	25.4	0.3	18.2	0.0	25.0	0.1	37.3	0.1

\* Frequency of occurrence (FO) indicates the number of nonempty stomachs in which the prey item was present in any amount. Abundance by weight (AW) indicates the percent of the total weight of stomach contents constituted by the prey item.

Taxonomic identification of prey items in the fish was limited due to the digested nature of many of the stomach contents. Because of this, most of the contents were grouped into fairly broad categories, generally not proceeding beyond the level of class or order. However, when a well preserved specimen was encountered, attempts were made to classify it as specifically as possible.

Table 3 is a taxonomic list of all the items that were found in the stomachs of both species of juvenile salmon. Detailed identification of items to the species level is presented where possible. However, the species presented should be considered as examples, and not a complete list. For the more specific taxonomic groups (family, genus, and species) the inclusion of one group does not imply that other groups were not consumed. They may have been present, and simply not identified due to their advanced state of digestion.

### Stomach Content Change Over Sampling Period: Coho

On examination of the food items taken by coho at different dates over the summer (Figure 4), two readily apparent changes in diet composition are seen. Early in the summer, terrestrial insects made up a large proportion of the coho diet (35% by the end of May).

Table 3. A taxonomic listing of items identified in smolts' stomachs

#### PHYLUM COELENTERATA

##### Class Hydrozoa

*Hemigrapsus nudus* (larvae)

*Hemigrapsus sp.* (larvae)

##### Section Anomura

Family Porcellanidae (larvae)

#### PHYLUM NEMATODA (as parasites)

*Anisakis sp.*

##### Class Arachnida

##### Class Insecta

Order Coleoptera (beetles)

Order Collembola (springtails)

Order Diptera (flies)

Family Tabanidae (larvae)

Order Hymenoptera (wasps)

#### PHYLUM ARTHROPODA

##### Class Crustacea

Subclass Ostracoda

*Conchoecia sp.*

Subclass Copepoda

Order Calanoida

*Acartia sp.*

*Epilabidocera sp.*

*Candacia sp.*

Order Cumacea

*Lamprops sp.*

Order Isopoda

*Gnorimosphaeroma sp.*

Order Amphipoda

SubOrder Gammaridea

*Elasmopus sp.*

*Stenothoides sp.*

*Stenothoides burbanki*

Suborder Caprellidae

Suborder Hyperiidea

*Hyperia sp.*

*Hyperiella sp.*

*Hyperiella macronyx*

Order Euphausiacea

*Euphausia pacifica*

Order Decapoda

Suborder Reptantia

Section Brachyura

Family Cancridae

*Cancer sp.* (larvae).

Family Grapsidae

#### PHYLUM MOLLUSCA

##### Class Cephalopoda

*Loligo sp.*

#### PHYLUM CHORDATA

##### Class Osteichthyes (larvae)

Family Clupeidae (herrings)

*Clupea harengus pallasii* (pacific herring)

Family Scorpaenidae (scorpionfishes)

*Sebastes sp.*

Family Hexagrammidae (greenlings)

Family Ammodytidae (sandlances)

*Ammodytes hexapterus*

Family Salmonidae (salmonids)

Family Pleuronectidae (righteye flounders)

#### PLANT MATTER

##### Phaeophyta (brown algae)

*Fucus sp.*

#### INORGANIC MATTER

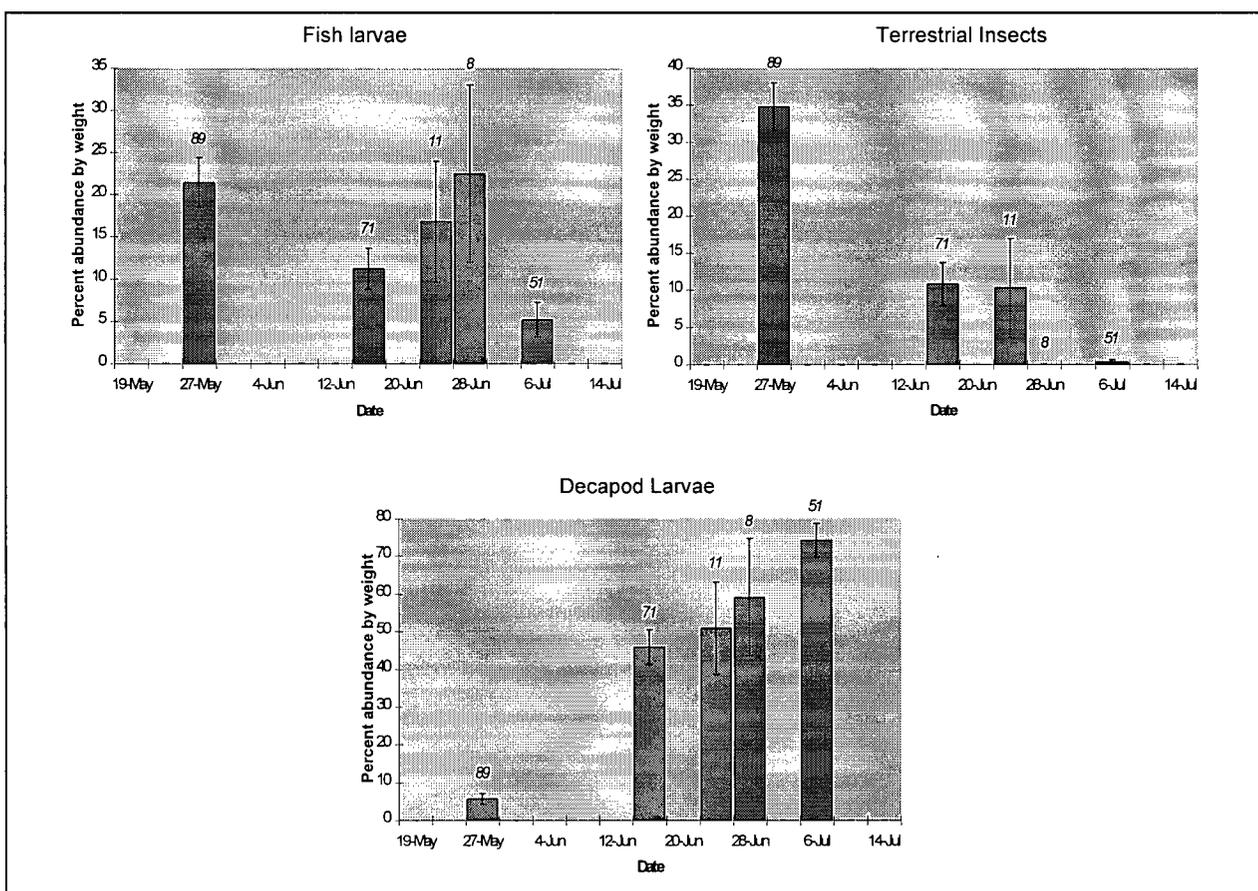
Wood

Plastics

Fishing Line

As the summer continued and insects became less important, brachyuran crab larvae became increasingly important, making up as much as 74% of the coho diet by the end of the sampling period. Larval fish comprised the other main constituent of the juvenile coho diet. These appeared to be an important food item throughout the sampling period. While the amount of fish larvae being eaten varied somewhat by date, they never made up less than 5% of the total diet by weight at any time.

Figure 4. Coho: Stomach abundance by weight of major prey items during the summer of 1993. Italics indicate sample sizes.



Since coho fork length increased regularly over the summer, the pattern of diet composition with respect to length is similar to diet composition with respect to date. Terrestrial insects were an important diet item in smaller coho, but as the fish got larger, they appeared to stop eating insects altogether. Conversely, the larger fish appeared

to be eating more brachyuran crab larvae than did smaller fish. Fish larvae were a significant diet component for almost all sizes of juvenile coho.

There is some suggestion that the very largest fish were eating almost exclusively crab larvae, and that fish larvae were a relatively unimportant diet item for these fish. However, it should be noted that the sample sizes of fish at the tails of the length distributions were small. Thus, the reduction in diet variation might have been due to the fact that, in some cases, only one or two fish were used to determine an average diet. In the middle size ranges, up to twenty five fish contributed to the sample of stomach contents.

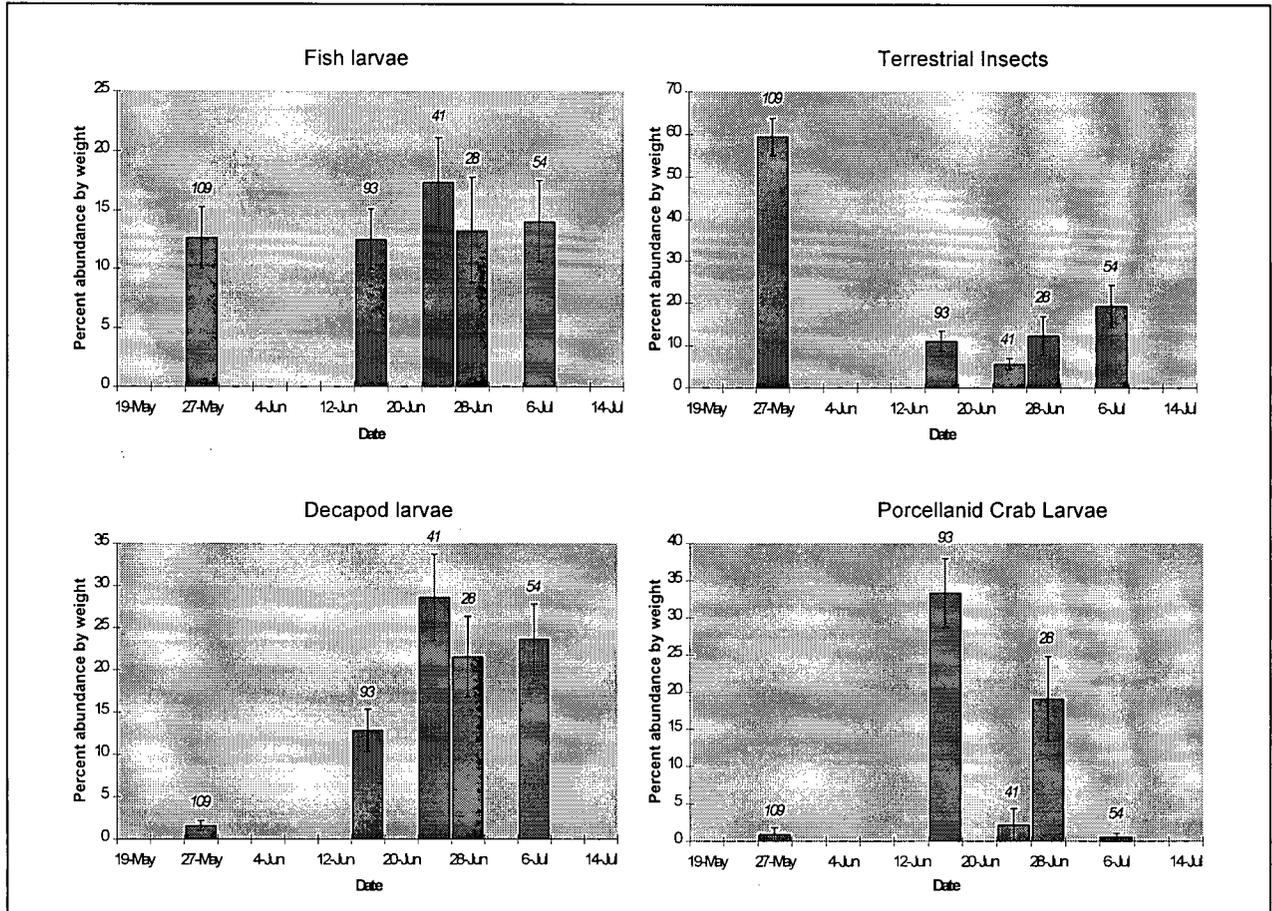
#### **Stomach Content Change Over Sampling Period: Chinook**

The pattern of food utilization was not as clear for juvenile chinook as it was for coho (Figure 5). Like the coho, early in the summer chinook appeared to be utilizing terrestrial insects to satisfy a high proportion of their dietary needs (60%). This proportion dropped off considerably as the summer continued, but at the latest sampling dates it increased again to 20%. Overall, it appears that the pattern of eating large amounts of terrestrial insects early in the summer, and fewer later on occurred in chinook as well as coho. However, the chinook ate more terrestrial insects at the earliest and latest sampling dates than the coho did.

Although it is not as regular or as dramatic as the pattern seen in the coho, juvenile chinook also appeared to be eating an increasing amount of brachyuran crab larvae as the summer continued. Unlike the coho however, the chinook also ate anomuran crab larvae (of the family porcellanidae) in significant amounts in the middle of the sampling period (up to 33% of the diet, by weight). Since the size and shape of the porcellanid larvae are considerably different than that of the brachyurans, it is assumed that juvenile salmonids would perceive these two species as distinct diet items.

With respect to fish larvae in the diets of the juvenile chinook salmon, more or less the same pattern occurred as was seen in the coho. Fish larvae continued to constitute a significant proportion of the diet throughout the sampling period. Figure 5 summarizes the variation in major prey items taken by chinook over the sampling period.

Figure 5. Chinook: Stomach abundance by weight of major prey items during the summer of 1993. Italics indicate sample sizes.



The increase in chinook fork length was not as regular over the sampling period as it was for coho. This may have been due to the confounding effects of 0+ and 1+ fish being mixed in the same samples. Nevertheless, when comparing diet composition with respect to fork length for chinook, it becomes clear that larger fish consumed fewer terrestrial insects than smaller fish. The only exception to this obvious pattern occurs at a fork length of 180-185mm, but since only one fish was sampled in this category, it is unclear as to whether or not this exception indicates a general pattern. The data for other fish around the same size suggest that terrestrial insects are not a common diet item for larger fish.

The increasing consumption of brachyuran crab larvae with increased chinook fork length is also quite evident from the data. While this pattern is not as pronounced as that seen for juvenile coho, it does appear that crab

larvae become a more important diet item as fish grow. Utilization of porcellanid crab larvae by the chinook appears to occur generally at the smaller size classes, but is coincident with the reduced use of insects as a food item. The largest size classes did not appear to be eating porcellanids.

Except for the very smallest chinook, most size classes appeared to be eating a significant proportion of fish larvae. Thus it appears that salmon of most of the sizes sampled were eating fish larvae throughout the entire sampling period.

Probably the most striking pattern that is apparent in the chinook diet composition vs. fork length comparison is the general increase in digested matter in the fish gut with increasing size. This may be due to the preservation method chosen, in that digestive enzymes in a larger fish may take longer to freeze and be inactivated than those in a smaller fish. However, the fact that a similar pattern was not seen in juvenile coho over a similar size range suggests that this is not the case. A simpler explanation presents itself when one considers the length/frequency distribution of juvenile chinook. Increased amounts of digested matter were found in size ranges where fewer fish were sampled. Therefore this is probably another reflection of reduced variability in diet composition due to a reduced number of guts contributing to the pool of sampled stomach contents.

### **2.2.3. Discussion of Stomach Contents Patterns**

Historically, most salmonid feeding studies have concentrated on fish at ages either older or younger than the target age for this study. Thus, many publications exist detailing dietary habits of adult salmon at sea, and juveniles in the fresh water or estuarine environment. However, there are relatively few that deal with juvenile salmon in the marine environment, and even fewer that concentrate on the Georgia Strait. Nevertheless, in order to carry out bioenergetics calculations, it was necessary to get a broader idea of normal feeding patterns for juvenile coho and chinook salmon in the Georgia Strait. Therefore, I compared the results of my feeding study with others similar to it, in order to see if some overall pattern could be discerned (Foskett 1950, Shapovalov 1954, Prakash 1962, LeBrasseur 1966, Manzer 1968 and 1969, Robinson 1969, Myers 1979, Healey 1980, Brodeur 1989).

### **Terrestrial Insects**

The utilization of a large proportion of insects is not unheard of among juvenile salmon feeding studies. However, insects have rarely been shown to be as important for both coho and chinook as they were in the current study. As early as 1950, Foskett reported a surprisingly large proportion of terrestrial insects in both coho and chinook caught in the Nanaimo area. Robinson (1969) showed juvenile fish in the Georgia Strait to be consuming an assemblage of insects remarkably similar to that in the current study. However, Manzer (1969) found diets of young coho in the Chatham sound area to have only about 5% insects. More recently, off the coast of Washington and Oregon, Brodeur (1989) found insects to constitute a high proportion of coho diets, similar to that shown in my study. However, he did not find that juvenile chinook were eating insects to any significant degree. Healey (1980), in the most comprehensive study of juvenile salmon in the Georgia Strait to date, did not find insects to be an important diet item for coho or chinook, with the exception of chinook rearing in the estuary.

Thus, the general picture with respect to the use of insects by juvenile salmon appears somewhat murky. No previous study has shown them to be utilized to the same degree, or for as much of the summer as was found in this study. This is particularly true for chinook, who have seldom been shown to be eating any significant proportion of terrestrial insects at all. A possible explanation was proposed by Brodeur (1989). He suggested that terrestrial insects were particularly abundant in salmon stomachs in times of unusual wind patterns. Presumably, insects were blown offshore, and trapped on the surface layer of salmon feeding grounds. It should also be noted that in the current study, insect use was much higher for both species in the early summer. This may represent a latent preference for insects in fish that have recently left the estuarine environment, where it has been shown that insects make up a large proportion of their diet (Healey, 1980, Anderson et al., 1981, Brown et al. 1987, Macdonald et al. 1987). Finally, the fact that a very large proportion of fish in the current study were caught either in or near to the Fraser River Plume may mean that they were presented with an unusually high proportion of terrestrial insects that were being carried out into the marine environment from further inland.

### **Fish Larvae**

Historically, the utilization of fish larvae as a diet item for juvenile salmonids is well documented. However, both the extent and timing of the consumption of fish are quite variable. In 1950, Foskett found that chinook and coho in the Nanaimo area started off eating smaller organisms, and then graduated to fish (mainly herring) as they grew in size. LeBrasseur (1966) showed that coho diets in coastal zones depended on fish for almost half of their prey. Manzer (1969) found that fish made up a very large proportion of juvenile coho diets (up to 70%) throughout the summer. Healey (1980) found that the utilization of fish was quite variable both by year and by area. Chinook were shown to feed more heavily on fish in late summer 1975 (63%) than in late summer 1976 (29%). He explained this difference as a reduction in availability of fish and showed it to be mirrored in other species. He also showed that chinook ate fish most heavily in the Gulf Islands (79%), while they were less important in the Fraser River Plume (37%) and the Central Strait. The same year to year variation was shown for coho, although overall fish were a less important contributor to their diet than to that of chinook. For both species, invertebrates were more important than fish earlier in the summer. Conversely, Brodeur (1989) found that coho ate more fish in June (19%) than they did in either July (5%) or September (6%). While chinook ate more fish at all three months than coho did, they showed the same pattern of decreasing amounts as the summer continued (34%, 30% and 16% for June, July and September respectively).

Again, it is difficult to draw a general conclusion from existing studies. It appears that fish are an important diet component, but their availability can be quite variable. Historically, it appears that chinook have eaten fish to a greater extent than coho, although the current study does not follow this pattern. It is interesting to note that more recent studies (including the current one) show lower overall levels of larval fish in the salmonid diets. This may simply be a random manifestation of the normal variability in fish availability. However, it is also possible that larval fish are being more heavily impacted as a food source as increasing numbers of juvenile salmon are released into the Strait every year from hatchery operations. It is also interesting to note that the general pattern observed in earlier studies, in which larval fish became an increasingly important food item as the summer wore on, is not borne out in the two most recent studies (Brodeur, 1989 and this one). Brodeur showed either a constant or

decreasing utilization of fish for both species, while the current study found a more or less constant use of larval fish throughout the summer.

### **Decapod Larvae and Crustaceans**

Decapod larvae, particularly anomuran and brachyuran crab larvae, are the only food item for which a relatively consistent pattern of consumption has been shown by feeding studies. Foskett (1950) defined the general pattern when he reported that juvenile salmon in the Nanaimo area gradually transferred to crustaceans as they graduated from insects and smaller prey. Prakash (1962) supported this pattern when he found crustaceans to be the main early summer diet of coho and chinook, followed by fish in later months. Manzer (1969) did not report this kind of progression, but did find decapod larvae to be one of the principle diet items of juvenile coho in Chatham Sound. Myers (1979) found that hatchery coho in channel areas fed on crab larvae to a greater extent than their wild counterparts. In June, Healey (1980) found that coho consumed crab larvae in June of 1968, but not 1966. Later in the summer he found *Cancer gracilis* megalops to be an important component in both of his study years. Healey showed that chinook ate decapod larvae throughout the summer, especially when fish larvae were scarce in their diet. For both species, crab larvae were more important in the Gulf Islands and the Fraser River Plume, and less important in fish that were caught further north in the Strait. Brodeur's (1989) study off the Washington coast runs somewhat contrary to the general pattern, in that he found coho to be eating decapod larvae at very high levels (67%) in June, with these levels falling off in July and September. Chinook were also seen to eat many decapods early on, and while the levels fell off somewhat, they remained relatively high throughout the summer.

Overall, except for Brodeur's (1989) study it appears that a general pattern can be discerned. Decapod larvae seem to replace the early invertebrate diet items (such as insects) as the juvenile salmon grow during the summer. In this study, and in Brodeur's, coho appeared to utilize decapod larvae to a greater degree than chinook, although Healey (1980) found chinook in some areas to have a very high proportion of crab megalops in their diet. Thus, in an otherwise variable diet picture, it appears that decapod larvae make up a consistently important fraction of juvenile coho and chinook diets.

### **Other diet itmes**

The diet items discussed so far were the main prey of the fish analyzed in the current study. Taken together, these items generally comprised 90% or more of the identifiable prey in the juvenile salmon stomachs. No other individual prey consistently made up more than 5% of the diet of either species. However, there are a few prey species that have been important in a number of historical studies, and were represented in my samples, which are worthy of mention.

Euphausiids have long been established as a major food item for adult coho and chinook salmon (Prakash, 1962, LeBrasseur, 1966, Manzer, 1968, Graham and Argue, 1972). Therefore, it is not surprising that they have appeared as an important item in some studies of juvenile salmon stomach contents as well. Healey (1980) found that in June, coho in the Saanich inlet used euphausiids as their main diet item. Coho showed a preference for euphausiids when their consumption levels were compared with those of other fish species. Brodeur (1989) showed euphausiids to be important for both coho and chinook. Unlike Healey, however, he found that euphausiids increased in importance later in the summer. By September they made up 24% of coho diets, and 41% of chinook diets. In light of the fact that euphausiids appear to be primarily an adult salmon food, this second pattern is more intuitive than that found by Healey. In the current study, euphausiids, while frequently present, were generally unimportant. Chinook appeared to eat a small amount (less than 1%) consistently, while coho were only seen to consume them early in the summer, when they made up 1% of the total diet.

Amphipods are another diet item that, while frequently observed in my samples, never made up a large proportion of the salmon diets by weight. Nevertheless, they too have been important in past studies of juvenile salmonid diets. Healey (1980) found them to be important for coho throughout the summer. Amphipods appeared to be eaten as a replacement for unavailable diet items, such as decapod larvae and fish. Amphipods were also important throughout the summer for chinook, again replacing fish when fish were unavailable. This was particularly true for the Fraser River Plume and the North Strait. In the Gulf Islands, amphipods were less important. Brodeur (1989) showed amphipods to be an increasingly important component of coho diets as the summer continued, making up over half of the volume of stomach contents in September. Chinook showed the

same general pattern, although amphipods did not attain as great an importance. Nevertheless, by September they composed 14% of the the stomach contents.

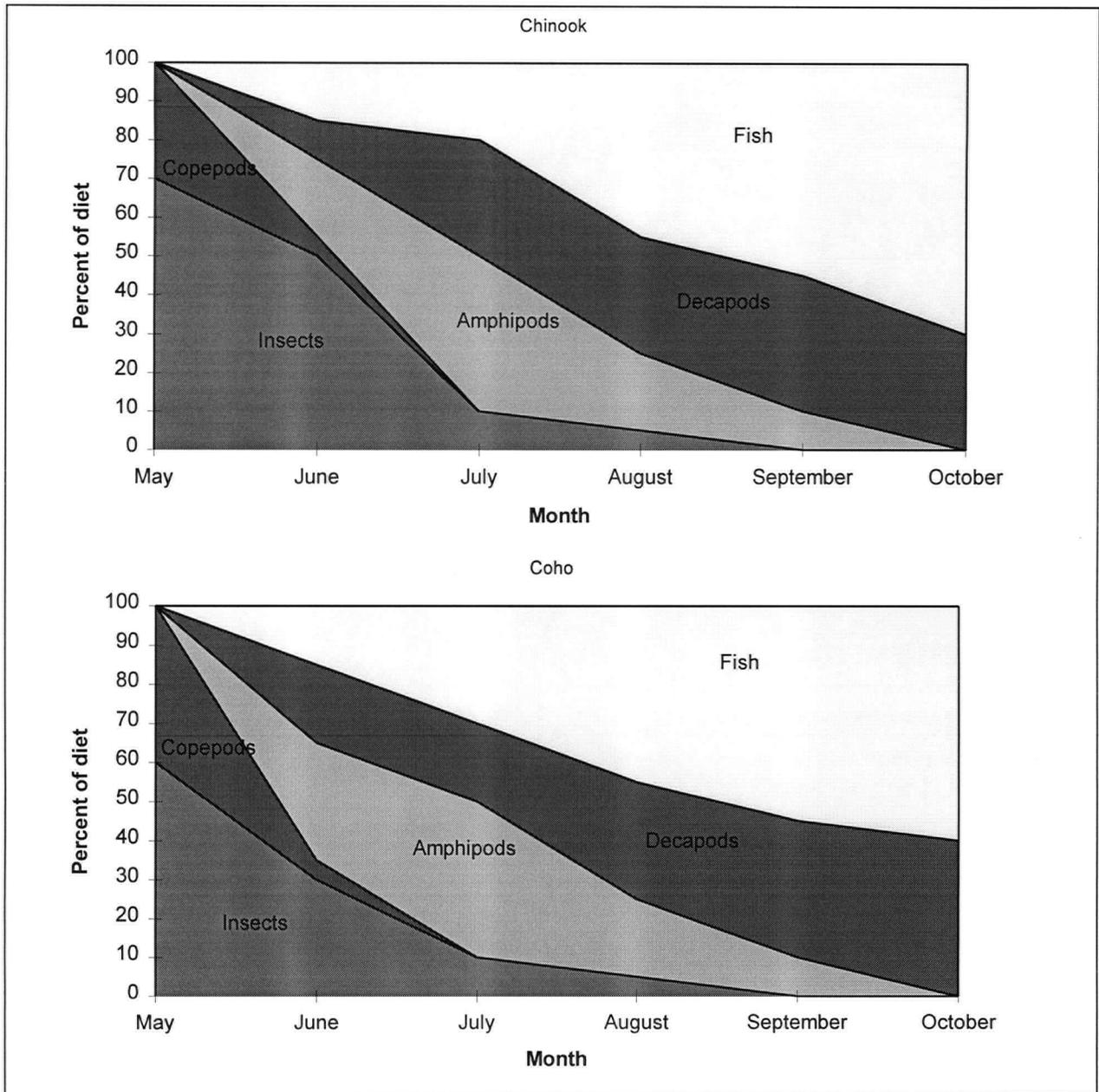
It is well established that copepods are an important food of juvenile salmonids before they enter the marine environment (Anderson et al., 1981, Macdonald et. al. 1987). Therefore, it is not surprising that some studies have found them to be of continued importance in the early ocean phase of the salmonid life cycle. Both Healey (1980) and Brodeur (1989) found that chinook and coho consumed copepods early in the summer in the marine environment. Interestingly, Healey found that copepods were less important to chinook than to coho, pinks, chums, and sockeye. Brodeur, on the other hand, saw copepods making up to 38% of chinook diets in July, while copepods never made up more than 7% of coho diets. Nonetheless, copepods were a much more important item in these studies than in the current one.

Finally, it should be noted that the pteropod mollusc *Limacina* was seen to be an important diet item for coho by both Healey (1978) and Brodeur (1989). This was particularly true in Healey (1980) for fish that were caught in the North Strait, where pteropods made up 20% of the coho diet. No *Limacina* were found in the stomachs of juvenile salmonids in the current study.

#### **2.2.4. Feeding Study Conclusions**

Given the available studies of juvenile coho and chinook salmon feeding, it is difficult to define any specific pattern of diet composition in the early months at sea. The overall picture is one of variability. This reinforces the generally held belief that salmonids are opportunistic feeders (Prakash 1962, Sandercock 1991). In the historical studies, the variability in diet compositions appears to follow availability of food items. However, using these studies, it is possible to define a few apparently preferred food items, and in this way produce a broad general picture of the feeding patterns.

Figure 6. Feeding regimes used in the bioenergetics model.



Most studies have shown a general pattern of starting with smaller invertebrates in the estuary, and moving through larger marine invertebrates to a more piscivorous diet as the summer continues (Shapovalov et al. 1954). The main exceptions to this pattern show that fish may be an important diet item throughout the summer. Food items that seem to be important in a majority of studies include terrestrial insects, decapod larvae, fish larvae, and,

to a lesser extent amphipods. The occurrence of these items is consistent for most studies. Most of the variability in consumption levels of any one prey type appears to occur in response to the availability of one or more of the other types. Because of their key importance in the diets of juvenile salmonids in the Georgia Strait, the diet items used to construct an idealized feeding regime were insects, copepods, decapods, fish and amphipods. This regime was used to define the consumption patterns incorporated in the bioenergetics model (section 2.4). Figure 6 illustrates these patterns for both coho and chinook.

## **2.3. VIRTUAL POPULATION ANALYSIS**

### **2.3.1. Introduction**

Virtual Population Analysis (VPA) is a straightforward technique that is used to estimate historical numbers of fish based on currently observed population sizes and removals. VPA relies on catch-at-age data to recursively calculate stock sizes based on catches. Calculations for each cohort are done individually. The standard procedure is to calculate the number of fish alive in each separate cohort for each past year. This is done based on the numbers of fish known to be alive in a given year, and assumed values of natural mortality and catch. The simple relationship used for each cohort is as follows (Hilborn and Walters, 1992):

$$N_t = N_{t+1} + C_t + M_t$$

where:

$N_t$  = the number of fish alive this year.

$N_{t+1}$  = the number of fish still alive next year.

$C_t$  = this year's catch.

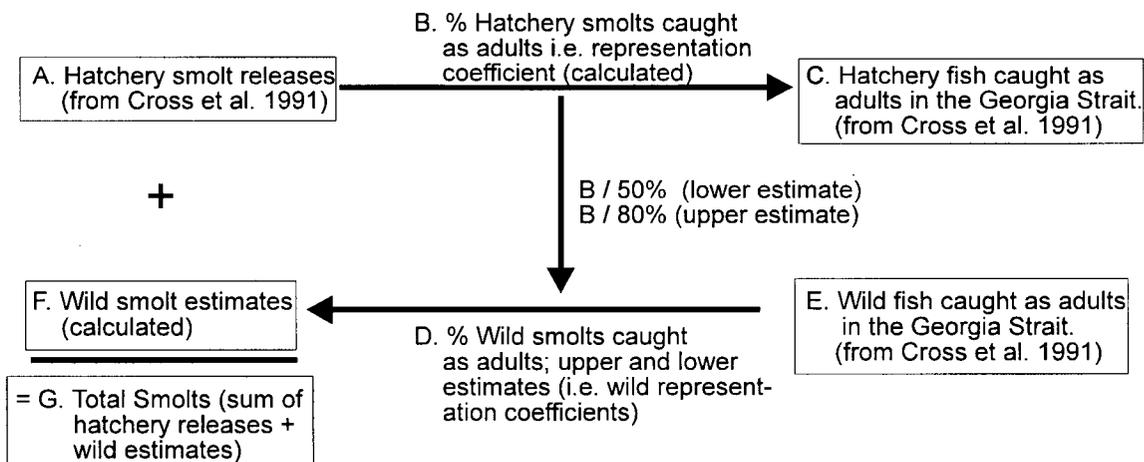
$M_t$  = this year's losses due to natural mortality.

Note that the above equation does not account directly for immigration and emigration, which CWT data show are important for most Georgia Strait stocks. To some extent emigration losses are balanced by immigration

from Puget Sound stocks; other emigration losses were included as part of the natural mortality figures used in the VPA procedure, so no confounding effects should have resulted from fish exiting the Strait.

In the current study, a modified form of the VPA was used to calculate the number of smolts that must have been present in the Strait to account for observed catch-at-age data. This modified VPA used "representation coefficients" in place of natural mortality estimates to recursively calculate smolt numbers. This method was considered superior to using estimates of smolt-to-adult mortality due to the variability and inherent biases in historical estimation procedures (Ricker 1976). While more recent studies have improved on instantaneous estimates of marine mortality (McGurk 1996), there are still few empirical estimates for chinook (Bradford 1995). The complete VPA procedure that was used is outlined below, and summarized in Figure 7.

Figure 7. Flow chart showing the procedure followed in the modified VPA. See text for further explanation.



### 2.3.2. Materials and Methods

The protocol for the modified VPA was based on data obtained from Cross et al. 1991. This report provides recent, relatively complete data for estimating hatchery smolt numbers entering the Strait. Included in it are detailed hatchery release data, Georgia Strait catch statistics from all fisheries (divided into hatchery and wild

contributions), and catch at age data for the Georgia Strait fisheries. All the data are presented for ten years or more, spanning from the mid seventies to the late eighties.

The first step in the modified VPA was to obtain an estimate of the numbers of hatchery smolts being released into the Georgia Strait ("A" in Figure 7, Table 4). The detailed hatchery release information in Cross et al. provided the numbers of fish released from all the hatcheries that enter the Strait. However, not all of these fish were released as smolts. Some were released as fed fry, and others as unfed fry. Therefore, released numbers of fry were multiplied by appropriate survival rates, to convert them to "smolt equivalents." For chinook, fry to smolt survivals were estimated at 30% for fed, and 10% for unfed fry (Healey 1991). For coho, fry to smolt survival was estimated at 1% for unfed, and at 7% for fed fry (Sandercock 1991). All the chinook fry were assumed to be ocean-type fish who migrate downstream to the estuary in the same year that they are hatched. Therefore, they were added to the smolt numbers in the same year that they were released. Coho, on the other hand, generally spend a year or more in fresh water before they enter the marine environment as smolts, so any fry released in a given year were survived and added into the total smolt releases for the following year. An example of the calculation of hatchery smolt releases for chinook is shown in Table 4.

The next step in the modified VPA was to determine the number of hatchery smolts from each year that contributed to later catch statistics drawn from Cross et al. (1991). This produced an adult "sample" (through catches) of hatchery smolts that allowed an estimation of "survival" of smolts to be caught as adults ("C" in Figure 7).

Smolts can go on to be caught as adults at more than one age. For example, chinook can be caught as 2, 3, 4 or 5 year old adults. Because of this, it was necessary to combine data showing the hatchery contribution to Georgia Strait catches with data that showed catch-at-age. By doing this, it was possible to apportion the hatchery contribution to catch into smolt production years. Thus, for each catch year it was possible to calculate how many smolts from each hatchery production year had contributed to it. An example of this procedure as performed for chinook smolts is shown in Table 5.

Table 4. Release of chinook juveniles from SEP facilities. Data from Cross et al. (1991)

Region	Stage	Smolt Year								
		1976	1977	1978	1979	1980	1981	1982	1983	1984
Inside	unfed fry	0	0	0	310160	0	0	0	222	0
	fed fry	0	0	726	70046	257855	270027	436942	263860	568620
	smolts	2466174	5329193	4661154	7785011	9423722	7523551	9607293	1.2E+07	1.3E+07
	effective smolts (survived fry)	2466174	5329193	4661372	7837041	9501079	7604559	9738376	1.2E+07	1.3E+07
Upper Fraser/ Thompson	unfed fry	0	0	0	0	0	2500	45000	0	0
	fed fry	0	16319	12963	34111	158857	198631	1470250	230091	915255
	smolts	0	0	0	14417	17753	56083	285620	1644009	3233352
	effective smolts (survived fry)	0	4895.7	3888.9	24650.3	65410.1	115922	731195	1713036	3507929
Total Strait Smolts		2466174	5334089	4665261	7861691	9566489	7720481	1E+07	1.4E+07	1.7E+07

The third step in the modified VPA was to produce a "representation coefficient" that served the same purpose as natural mortality rates do in a standard VPA ("B" in Figure 7). The representation coefficient method was preferable to using mortality rate estimates, since existing mortality estimates are quite variable, and not specific to the salmon populations in the Georgia Strait. The coefficient was produced by dividing hatchery contributions to catches by the numbers of hatchery smolts released. Thus, it provided an index as to how likely it was that a smolt from a given year would turn up in the Georgia Strait catch in a later year. In reality, it is a composite that represents loss of smolts to many different agents, probably the most important of which is natural mortality. However, other agents that might prevent a smolt from being represented in later Georgia Strait catches include escapement to spawning, catches in other fisheries outside the Georgia Strait, and straying to other river systems (i.e. emigration). Nonetheless, the representation coefficient provides a direct index of the likelihood of a given fish making it from the smolt stage into the catch "sample" as an adult. It should be noted that the coefficient was calculated for the likelihood that any smolt would end up in any catch year. For example, a hatchery chinook smolt from 1981 had a 0.11% chance of showing up in the 1982 catch, a 0.23% chance in the 1983 catch, a 0.31% chance in the 1984 catch and a 0.05% chance of being caught in 1985. Chinook smolts from 1981 did not show up in catches from any other year. Table 6 shows an example of representation coefficients as calculated for chinook

hatchery smolts. It can be seen from the format that Table 6 is simply derived from the information presented in Tables 4 and 5.

*Table 5. Chinook salmon: adult hatchery catch contributions broken down by smolt year and catch year. Data from Cross et al (1991)*

Smolt Year	Catch Year												Total Caught	
	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989		
1974	4881													**
1975	23796	4435												**
1976	20135	21620	3572											**
1977	12203	18294	17411	4063										51971
1978		11087	14733	19806	3518									49144
1979			8929	16759	17152	4386								47225
1980				10157	14513	21382	4883							50934
1981					8796	18092	23802	3596						54286
1982						10965	20141	17529	3962					52597
1983							12206	14833	19316	2678				49033
1984								8989	16344	13056	2561			40950
1985									9905	11047	12483	3992		37427
1986										6695	10562	19462		**
1987											6401	16468		**
1988												9981		**

*\*\*note that for the first three and last three smolt years, the total number of smolts represented in catches could not be calculated. This is because chinook are caught as two, three, four, and five year-olds. Therefore, some fish from each of these smolt years would be caught in years for which catch statistics were not available.*

Once these representation coefficients had been calculated, they were used in conjunction with the wild contributions to each catch year (Cross et al. 1991, "E" in Figure 7) to back-calculate the number of wild smolts that must have been present to produce the observed catches. It was tempting to simply use the same representation coefficient values as were calculated for the hatchery smolts. However, it is commonly accepted that hatchery smolts have a lower survival to adult stages than wild smolts do (Nickelson 1986, Cross et al. 1991). Among studies that have attempted to quantify this reduction in hatchery smolt to adult survival, most have found that hatchery survival is somewhere in the range of 50 - 80% that of wild smolts (Cross et al. 1991, Parkinson 1995).

Table 6. Chinook salmon; percent of each hatchery smolt year represented in each catch (representation coefficients).

Smolt Year	Catch Year												Total % Caught	
	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989		
1974	1.21%													
1975	1.16%	0.22%												
1976	0.82%	0.88%	0.14%											
1977	0.23%	0.34%	0.33%	0.08%										0.97%
1978		0.24%	0.32%	0.42%	0.08%									1.05%
1979			0.11%	0.21%	0.22%	0.06%								0.60%
1980				0.11%	0.15%	0.22%	0.05%							0.53%
1981					0.11%	0.23%	0.31%	0.05%						0.70%
1982						0.10%	0.19%	0.17%	0.04%					0.50%
1983							0.09%	0.11%	0.14%	0.02%				0.36%
1984								0.05%	0.10%	0.08%	0.02%			0.24%
1985									0.04%	0.05%	0.06%	0.02%		0.17%
1986										0.02%	0.04%	0.07%		
1987											0.02%	0.05%		
1988													0.03%	

Therefore, to avoid over-estimating the numbers of wild smolts, the representation coefficients were adjusted to reflect the superior wild survival rates. In order to define a set of boundaries on the possible wild smolt population, representation coefficients were divided by both 0.5 and 0.8 ("D" in Figure 7). Table 7 shows representation coefficients for wild chinook, assuming hatchery survival to be 80% that of wild. Note that these values are simply those presented in Table 6, divided by 0.8.

Thus, two sets of wild smolt estimates were produced. The first was an upper boundary, defining a large population, in which the hatchery smolt to adult survival was 80% that of the wild smolts. The second described a lower boundary defining a smaller smolt population, in which the hatchery smolt to adult survival was 50% that of the wild smolts.

It should be re-emphasized that the representation coefficients are comprised of *all* the factors that would reduce a smolt's chances of later being represented in the Georgia Strait catch, and not just natural mortality. However, natural mortality is the only agent that should be different for wild and hatchery smolts. In other words, both types of smolts should have more or less the same chances of being caught in another fishery, or escaping to

spawn. Therefore, by adjusting the representation coefficients as though they *only* reflected natural mortality, I ignored the importance of these other agents. This means that the resulting wild smolt population estimates are probably a conservative under-estimation. This is especially true for the coho stocks. This however, is preferable to an over-estimation, in light of the fact that these numbers were used to investigate a potential carrying capacity limit. Nevertheless, it means that the large population estimates are probably a better estimate of the true coho numbers than the small population estimates, as both would be conservative to begin with. There is some possibility that wild chinook stocks were not subject to the same declining trend as evident for hatchery fish (Walters 1995). If this is true, then the chinook smolt estimates would not be as conservative as the coho estimates.

Table 7. Chinook salmon; percent representation of wild smolts in catches, assuming that hatchery smolts survive 80% as well as wild smolts to be caught as adults.

Smolt Year	Catch Year												Total % Caught	
	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989		
1974	1.51%													
1975	1.45%	0.27%												
1976	1.02%	1.10%	0.18%											
1977	0.29%	0.43%	0.41%	0.10%										1.22%
1978		0.30%	0.39%	0.53%	0.09%									1.32%
1979			0.14%	0.27%	0.27%	0.07%								0.75%
1980				0.13%	0.19%	0.28%	0.06%							0.67%
1981					0.14%	0.29%	0.39%	0.06%						0.88%
1982						0.13%	0.24%	0.21%	0.05%					0.63%
1983							0.11%	0.14%	0.18%	0.02%				0.45%
1984								0.07%	0.12%	0.10%	0.02%			0.30%
1985									0.06%	0.06%	0.07%	0.02%		0.21%
1986										0.03%	0.05%	0.08%		
1987											0.02%	0.06%		
1988													0.04%	

Once the upper and lower boundary representation coefficients had been produced for the wild smolt populations, it was a simple matter to back-calculate from the catch-at-age data to produce estimates of the wild smolt populations in the earlier years ("F" in Figure 7). Table 8 shows the catch-at-age-data used for chinook adults (Cross et. al 1991).

Table 8. Chinook salmon; number of adults in each catch year that originated in each smolt year. Data adapted from Cross et. al 1991.

Smolt Year	Catch Year											Total Caught	
	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988		1989
1974	209501												
1975	233674	200817											
1976	221588	223988	176809										
1977	141010	212403	197210	141017									691639
1978		135165	187009	157288	99293								578755
1979			119006	149152	110750	87651							466559
1980				94915	105022	97765	125639						423341
1981					66832	92708	140136	96061					395737
1982						58996	132888	107145	75996				375025
1983							84565	101603	84765	44103			315035
1984								64656	80380	49191	35786		230013
1985									51151	46647	39915	52745	190458
1986										29684	37850	58831	
1987											24086	55788	
1988												35501	

Since each catch year was comprised of fish that were smolts in several different years, and representation coefficients were produced for each smolt year to each catch year, several estimates of wild smolt population size were produced for each smolt year. For the most part, these estimates were reasonably close to each other. Therefore, they were averaged to produce a single estimate, and it was this wild smolt estimate that was added to the published hatchery smolt releases to produce a total estimate of the numbers of smolts that were present in the Strait in any given year ("G" in Figure7). Table 9 shows the estimates produced for chinook smolts.

Table 9. Chinook smolts; estimates of wild smolt population sizes derived from catch statistics and representation coefficients.

Smolt Year	Catch Year											Average estimate	
	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988		1989
1974	4279141												
1975	2.2E+07	2.3E+07											
1976	2.6E+07	2.7E+07	3E+07										
1977	5.6E+07	5.9E+07	6.5E+07	4.6E+07									5.7E+07
1978		5.2E+07	5.7E+07	4E+07	3.2E+07								4.5E+07
1979			9.6E+07	6.7E+07	5.5E+07	3.9E+07							6.4E+07
1980				8.2E+07	6.6E+07	4.7E+07	6E+07						6.4E+07
1981					5.4E+07	3.8E+07	4.9E+07	5.1E+07					4.8E+07
1982						5.2E+07	6.6E+07	6.9E+07	4.9E+07				5.9E+07
1983							8.6E+07	9E+07	6.4E+07	5.5E+07			7.4E+07
1984								1.1E+08	7.9E+07	6.8E+07	5.8E+07		7.9E+07
1985									1.1E+08	9.1E+07	7.7E+07	7.3E+07	8.7E+07
1986										1.2E+08	1E+08	9.4E+07	
1987											1.2E+08	1.1E+08	
1988													1.1E+08

### 2.3.3. Discussion of VPA Results

#### Chinook

The primary objective in performing the VPA was to produce an estimate of total Georgia Strait smolt numbers that could be used in conjunction with a bioenergetics model in order to calculate total amounts of food required by the smolts. This task was made somewhat more complicated in that instead of producing a static picture of the numbers of smolts entering the Strait over the years, obvious trends in those numbers became apparent for both coho and chinook.

The chinook estimates for the upper boundary, in particular, showed an interesting pattern. From 1977 to 1985 the estimated numbers of smolts necessary to produce observed catches has increased somewhat (Figure 8). This is in spite of the fact that overall chinook catches have decreased substantially over that same period (Figure 1). This implies that smolt to adult survivals could have been decreasing even more dramatically than one would expect given the relative amounts of known smolt releases and adult catches. In other words, survivals would have to have

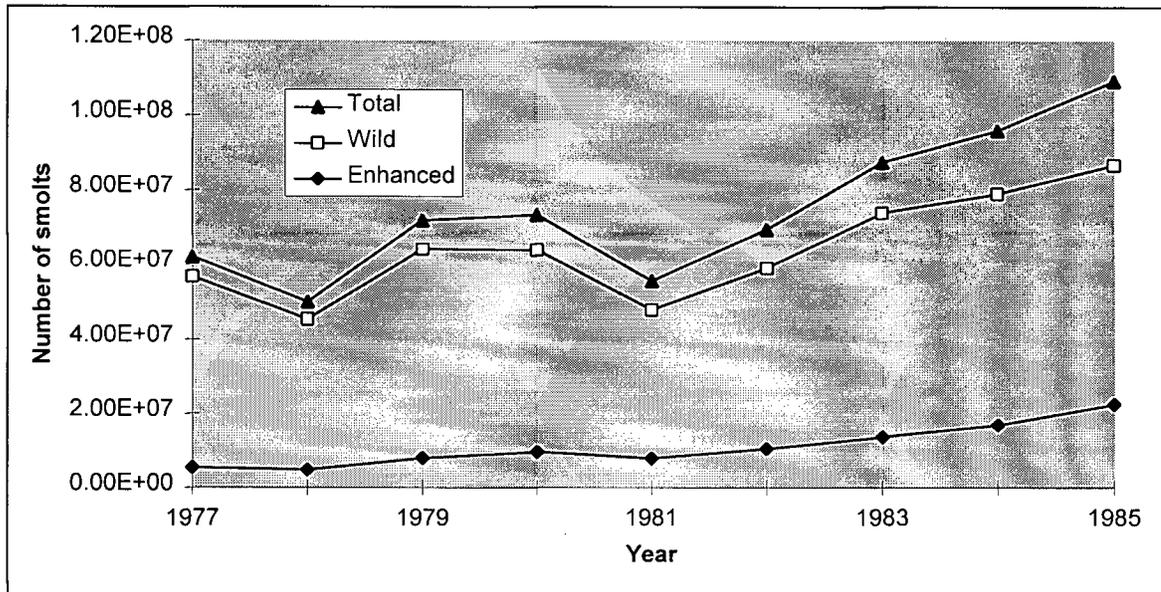
decreased to such an extent that not only are more smolts necessary to produce a constant number of adults, but more smolts are necessary to produce even fewer adults.

It is possible that this result is simply an artifact of the estimation method chosen, if in fact the ratio of hatchery to wild representation coefficients was not constant over this period. This could only be the case if the ratio of hatchery to wild survivals was decreasing during this time, as would occur if survival rates have not declined as violently for wild chinook as for the hatchery smolts. Any other agent that reduced representation coefficients would be expected to affect both hatchery and wild stocks equally, and so the ratio of the two would stay the same. For example, if more hatchery fish were being caught in fisheries outside the Strait, the same would be true of wild fish, so that the relationship between their representation coefficients would be the same. In the case of natural survival however, it is possible that hatchery smolt survivals were becoming poorer relative to wild smolts over this period, so that the increase in hatchery smolts necessary to produce observed hatchery adults should not be mirrored by wild stocks.

An alarming pattern that was observed in my estimates of smolt numbers involved the ratio of wild to hatchery smolts entering the Strait over the years. While both hatchery and wild smolts entries were seen to increase, hatchery smolt numbers have been increasing at a faster rate than wild smolt numbers. This means that, if we use the large smolt population estimates, the ratio of wild to hatchery smolts decreased from 85% wild and 15% hatchery in 1977 to 71% wild and 28% hatchery by 1985. If this rate has remained constant, we could expect a ratio of 64% wild smolts and 36% hatchery smolts entering the Strait in 1995. This pattern becomes even more pronounced if it is not accepted that wild survivals have decreased as much as hatchery survivals in the Strait. If wild chinook survivals are assumed to be constant, then the wild smolt population estimates are reduced. Therefore the ratio of hatchery to wild smolts is increased.

The overall picture then, is one of total adult chinook numbers in the Strait falling. At the same time smolt to adult survivals also appear to be falling at an extremely rapid rate, at least for the hatchery stocks. It is unclear whether or not the wild survivals have decreased to the same extent. Either way, the result is that the estimates in the total number of smolts necessary to produce the observed adults has been increasing.

Figure 8. Chinook salmon; upper bound estimates of number of smolts entering the Georgia Strait, assuming 80% ratio of hatchery to wild survival.



Because of this increasing trend, I used the most recent estimates of smolt numbers in the bioenergetics model. These estimates were assumed to be most representative of the current situation. At the same time, they were among the highest over the entire period. Thus the situation they model is one in which a carrying capacity limit is most likely to be encountered. The estimates used in the bioenergetics model for chinook smolt numbers in the Strait were 100 million smolts in the small population estimate, and 150 million in the large population estimate.

### Coho

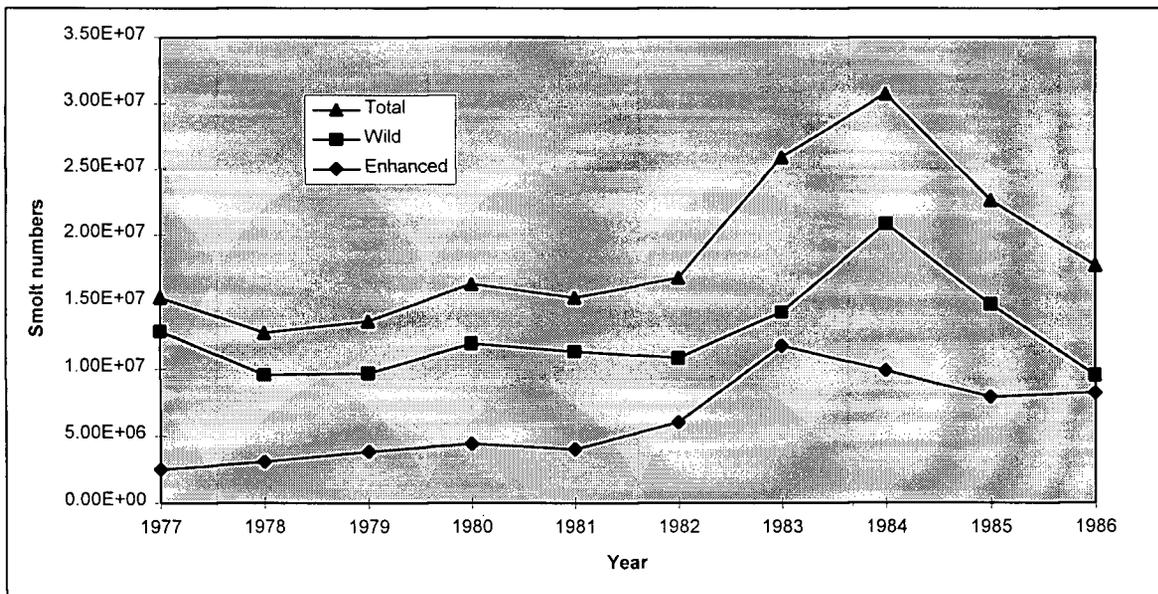
In estimating coho smolt numbers entering the Georgia Strait, the trends in population parameters were not as consistent as those seen for chinook. The declining catch statistics seen for chinook were mirrored by the coho only until 1984. After that, coho catches in the Strait recovered and stabilized somewhat.

The coho smolt estimates were similar to the chinook estimates in that they showed some increase from 1976 to 1988. However, this increase was not as consistent or as extreme as that estimated for chinook. The most striking feature of the smolt estimates is the extreme spike that occurs around 1984. This peak is due to the

recovery in coho catch coupled with a year in which the recruitment to the catch (as indexed by the representation coefficient) was quite low. This peak estimate suggests a total of up to 30 million smolts entered the Strait in 1984.

The proportion of hatchery/wild smolts entering the strait shows an increase that is even more dramatic than that seen in the chinook population. For the coho population, the increasing number of smolts entering the Strait appears to be almost entirely due to an increase in the number of hatchery smolts being released. The wild smolt estimates fluctuate over the same period, but do not show any consistent trend towards an increase or a decrease. The result of this is that, if we use the large population estimates, the proportions of coho smolts entering the Strait have gone from about 85% wild and 15% hatchery in 1977 to about 55% wild and 45% hatchery in 1986. Using the small population estimates, the 1986 smolts were more or less composed of equal parts hatchery and wild fish.

Figure 9. Coho salmon; upper bound estimates of number of smolts entering the Georgia Strait, assuming 80% ratio of hatchery to wild survival.



Once again, the overall pattern appears to be one of increasing numbers of smolts entering the Strait each year. In contrast to the chinook situation however, this increase does not appear to be due as much to decreasing survival rates of the smolts. Instead, most of it is explained by the increasing numbers of coho smolts being

released by hatchery operations around the Strait. Like the situation seen with the chinook population, the decrease in the estimated proportion of wild coho smolts entering the Strait appears to be significant.

The coho smolt numbers chosen to be used in the bioenergetics model were as follows: 15 million for the lower estimate, and 30 million for the upper estimate. These values encompass the variation seen in the coho smolt estimates in recent years. Thus, they were assumed to be the best available estimates of the current situation.

## **2.4. BIOENERGETICS**

A bioenergetics modelling procedure was used to estimate the amount of food energy that a smolt would need to consume in order to produce observed growth rates. This estimation was based on the balanced energy equation (Kitchell 1983, Ney 1990):

$$\text{Consumption} = \text{Growth} + \text{Respiration} + \text{Egestion} + \text{Excretion}$$

This equation is a mathematical expression of the idea that all the food consumed by an organism can be apportioned out to the physiological processes occurring in that organism. Therefore, food is either incorporated into biomass (growth) or energy (respiration), or is removed as waste (egestion and excretion). Given that all of the physiological parameters on the right side of the equation can be estimated from field or laboratory data, the model was used to produce consumption estimates specifically for coho and chinook smolts in the Georgia Strait. Since the VPA had produced estimates of total smolt numbers in the Strait, it was then possible to extrapolate and estimate the total amount of calories being consumed by salmonid smolts in the Georgia Strait. The bioenergetics modelling incorporated the first six months of the smolt's marine life, since it is during this time that they are consuming a juvenile diet consistent with that found in the stomach content analysis.

### **2.4.1. Materials and Methods**

The bioenergetics model used was "Fish Bioenergetics 2" produced by Hewett and Johnson of the University of Wisconsin. This versatile model comes equipped with physiological parameters for 20 different fishes. Among these taxa are many of the major Pacific salmonids, including coho, chinook, pink, sockeye, and lake trout. A complete description of the parameters used for all of the taxa, and their alternatives, is provided in

Chapter 3 of the Fish Bioenergetics User's Manual (Hewett and Johnson, 1992). In the following sections, I will describe the equations that were used for the coho and chinook modelling runs as they appear in that chapter. I will also describe the parameters that are not included by default in the model, such as feeding patterns and ocean temperatures. These were obtained from separate sources, and input to the model as external data.

### **Consumption**

Several options for consumption equations are included in the model. Their general form is to calculate the daily maximum specific feeding rate as a function of weight (g prey/g body wt.). This maximum rate is then modified by a temperature dependence function ( $f(T)$ ), and by an index of prey availability, expressed as a proportionality constant, or P-value. This P-value is a proportion of the maximum feeding rate actually exhibited by fish, which depends upon factors like food availability and activity level. The basic form of the overall consumption equation is:

$$\text{Consumption} = \text{Max. consumption} \times \text{P-value} \times f(T)$$

The bioenergetics model includes three options for the water temperature dependence function,  $f(T)$ . The actual equation used was the default included in the model for both coho and chinook. This is the Thornton and Lessem (1978) function, which provides a good fit for cold water species at low water temperatures. It calculates temperature effects as the product of two sigmoid curves; one half fits the increasing portion of the water temperature dependence curve (KA), and the other half the decreasing portion (KB). Thus the general form of the curve is:

$$f(T) = KA \times KB$$

The general result of using this algorithm is to increase consumption as temperature is increased from some low level. This continues up to an optimum temperature, after which consumption falls off rapidly as water temperatures increase to stressful levels. Details of the form of the two curves KA and KB, and the parameters used, can be found in Chapter 3 and Appendix 3 of the user's manual. The same curve, and parameters, were used for both coho and chinook, as was done by Stewart et al. (1981).

### Respiration and Specific Dynamic Action

Respiration is an expression of the amount of energy that a fish uses for metabolism. In the bioenergetics model, it is determined by calculating resting metabolism as a function of fish weight. This value is then corrected by a water temperature dependent factor, and another factor that represents activity. Finally, the energy lost to specific dynamic action is calculated (SDA). This is an expression of the metabolic heat lost from the digestion and transformation of food. This is added to the respiration value to produce a total metabolic rate. "Fish bioenergetics 2" models specific dynamic action as a constant proportion of the assimilated energy (i.e. that energy not lost to egestion or excretion).

Thus, the basic equation for determining total metabolic rate is:

$$R = (\alpha \times W^\beta \times f(T) \times \text{Activity}) + \text{Energy lost to SDA}$$

where:

R = the total metabolic rate

W = fish weight

$\alpha$  = intercept of the weight function

$\beta$  = slope of the weight function

f(T) = water temperature dependence function

Activity = increment for active metabolism

The bioenergetics model provides two temperature dependence functions, of which the first was used for both coho and chinook. This algorithm calculates water temperature dependence as a simple exponential function (Hewett and Johnson. 1992, Chapter 3). The model computes activity by using the swimming speed function developed by Stewart et al. (1983).

### **Egestion and excretion - losses due to waste**

Egestion is an expression of fecal waste, while excretion is the nitrogenous portion of the waste. The bioenergetics model allows these waste losses to be calculated in one of two ways: either as a function of water temperature and consumption, or more simply as a constant proportion of consumption. For both chinook and coho the first method was used.

The equation used also allowed for corrections depending on the digestibility of the prey item eaten. Prey items are entered into a separate file, and read into this equation. This allows the model to vary egestion and excretion depending on the prey that is being consumed. The equation that was used is described in detail in Chapter 3 of the User's Manual, and also in Stewart et al. 1983.

### **Growth**

Once the energy losses due to metabolism, egestion, and excretion have been accounted for, the rest of the consumed energy is transferred into growth of the fish. The balance of energy can be either positive or negative in the model, so that fish can either grow or lose weight, depending on the rest of the energy budget.

In the specific case of my modelling runs, growth was calculated using start and end weights that I supplied to the model as external parameters. The first step in estimating these start and end weights was to decide on corresponding lengths that were representative for chinook and coho populations.

From my 1993 catches of chinook in the Strait, the average length of smolts entering the Strait was 70 mm. Healey (1980) found the average length of chinook entering the Strait to be 80 mm. Thus, for the chinook start length, an average of these two was used, producing a value of 75 mm.

Healey (1980) also found that during their first six months in the Strait, chinook grow an average of about 0.8 mm per day. Therefore, at a start length of 70 mm, after six months in the Strait an average chinook will have reached a length of 214 mm. Using the same data, Healey defined a length/weight relationship for chinook as follows:

$$\text{Weight(g)} = 3.53 \times 10^{-6} \times \text{Length(mm)}^{3.282}$$

This relationship was used to convert the observed start length, and the calculated end length into weights. The start and end weights that were used for chinook in the bioenergetics modelling runs were 4.01 g and 157.11 g

The same process was used to determine start and end weights for coho salmon. Once again using Healey's and my data, the start length for coho smolts entering the Strait was estimated at an average of 100 mm. The best estimates of coho growth over the range 100-280 mm are about 1mm/day (Healey, 1980). Thus after six months, the end length would be 280 mm. Healey defined the length to weight relationship for coho smolts as:

$$\text{Weight (g)} = 1.62 \times 10^{-6} \times \text{Length}^{3.42}$$

Thus the start weight (at 100 mm) for coho is 11.21g. The end weight (at 280 mm) is 379.14 g.

The bioenergetics model uses these start and end weights, over a user-specified time period, to calculate growth as a rate. This rate is expressed as grams of growth per day. The weight gain of the fish can be converted to an energy expression using an energy density (calories/gram, wet weight). The fish bioenergetics model calculates the energy density of both coho and chinook as a function of their body weight, using a simple linear regression, of the form:

$$\text{Energy density} = \alpha + \beta \times \text{Weight}$$

where:

$\alpha$  = the intercept

$\beta$  = the slope

In fact, two separate sets of  $\alpha$  and  $\beta$  values are supplied, in order to define different caloric densities for the predators as they enter different size ranges. However, the default cut off between the size ranges is 4000 g. Since I

only modelled fish which were smaller than this size, their energy densities were all defined by the same linear regression, using an intercept of 1377 cal/g, and a slope of 0.2356 for both species.

### **External data**

To this point, I have described the equations and parameters that are used as defaults in the fish bioenergetics model. All of these defaults are set by the model programmers according to the current state of knowledge regarding the general physiology of chinook and coho salmon. However, there are several sets of situation specific parameters that must be supplied by the user in order to perform a bioenergetics modelling run.

### **Temperature**

As already mentioned, the consumption, respiration, and egestion/excretion equations all have a temperature dependent expression involved in them. Thus, in order to make these expressions perform in a realistic fashion, it is necessary to have as detailed information on the temperature regimes in the smolt's environment as possible.

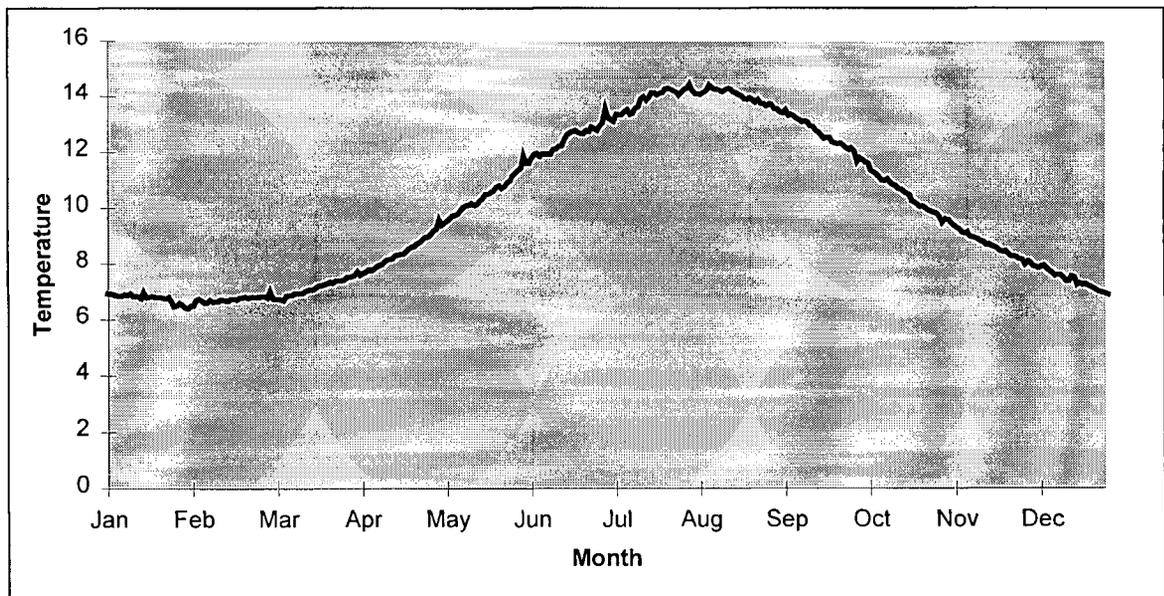
This information was obtained from lighthouse data collected around the Georgia Strait. Data collected from 38 lighthouses, some spanning up to 65 years, was averaged to produce a representative yearly temperature regime for the Georgia Strait (see Figure 10). The detail provided by this large amount of information allowed the temperatures used in the model to be remarkably realistic.

However, it should be noted that no weighting of values was done; that is, older data were given the same emphasis as more recent values. Thus, any possible effects of ocean warming trends were not considered. If temperatures in the Strait are increasingly significantly, or if a single year experiences higher than normal temperatures due to an El Nino event, observable differences in the bioenergetics model output would result. The temperature dependent factors would increase energy lost to respiration, egestion, and excretion. The net result would be an increased consumption of prey items in order to produce the same amount of growth in coho and chinook smolts. Therefore, if such warming effects are occurring, my estimates of prey consumption by salmon smolts would be low. This is important, since higher rates of prey consumption are more likely to produce a

carrying capacity limit. However, it is as yet unclear whether increased ocean temperatures are a permanent effect, or simply a transient variation in a long term pattern. Therefore, I chose to take a longer term view of the temperature patterns in the Strait, thereby modelling a more general situation. Also, by using the long term average, I maintained my policy of erring on the conservative side in all estimates that would contribute to the final consumption values.

Another reason for using the lower temperature regime dictated by the long term average is the probability that fish are seldom feeding right on the surface where the temperature data were obtained. Brodeur and Francis (1992) used temperatures that were several degrees below that at the surface, to simulate the temperature at a depth of 10 m, which was the midpoint of their sampling depth. Since the midpoint of my sampling depth was just under four metres, I did not feel that it would be valid to lower my temperature regime by an equivalent amount. Nevertheless, I feel that this further justifies not incorporating the average 1°C rise in temperature observed in local waters since the late '70s.

*Figure 10. Temperature regime used in the bioenergetics model.*



### **Diet patterns**

As already stated the goal of the using the bioenergetics model was to produce estimates of prey consumption from observed growth patterns of coho and chinook salmon. In order to do this, it was necessary to produce a representative diet regime for both coho and chinook. As explained above, estimation of the diet patterns of coho and chinook smolts was accomplished by analyzing the stomach contents of smolts from the Georgia Strait, and combining these results with the results of past sampling projects. The idealized feeding regimes produced followed the general pattern already described: an early emphasis on smaller food organisms such as insects and copepods, being replaced by larger organisms such as decapod and fish larvae, later in the summer (see Figure 6). Amphipods were used to represent smaller crustaceans being consumed before the later emphasis on the larger decapods, mainly in the form of crab larvae.

### **Prey Energy Densities**

Since the bioenergetics model converts wet weights of prey into energy used by the predator fish, it was necessary to provide the program with estimates of energy density (calories/gram wet weight) for the prey items used. All of the prey energy densities used were obtained from an extensive calorimetry study in the literature, in which thousands of representative organisms were burned to determine their caloric content (Cummins and Wuycheck, 1971). This source was also used to double check the default energy densities used by the model for the coho and chinook smolts that were feeding on these prey.

An added advantage to modelling prey as simple bundles of calories is that it reduces the variability necessary in the diet pattern used. This is due to the fact that many small marine invertebrates have similar energy densities. For example, the amphipods used in the idealized feeding pattern are intended to represent all similarly sized crustacean invertebrates. Thus, the five prey items actually used are not meant to be a complete list of everything a coho or chinook smolt might eat during their first six months at sea. Instead, they are representatives of the changes in prey energy densities thought to be consumed by smolts during their early ocean residence. Nevertheless, these five prey items do tend to comprise most of the stomach contents of coho and chinook examined in smolt feeding studies.

### **Mortality Estimates**

By using the modified VPA described earlier, estimates of the total numbers of smolts entering the Strait in a representative year were produced. However, it would be unrealistic to assume that all of these smolts continue to feed throughout the summer months. In fact, Healey (1991) suggests that most of the mortality that affects chinook salmon between their smolt and adult stages impacts the fish in their first year at sea. Parker (1962) supports this idea with his observation that predation mortality is concentrated in the coastal zone, where smolts in their early ocean life spend most of their time feeding. He also points out that salmon at smaller sizes are more susceptible to predation than larger ones. This idea is echoed by McGurk (1996) in his study of the allometric relationship between mortality and salmon size. Because of the undoubtedly high mortality of young salmon, it was necessary to include estimates of mortality for both coho and chinook during the six months over which they were modelled. This allowed the model to reduce the numbers of fish feeding in the Strait by appropriate amounts each day.

Using tag and recovery data, many authors have attempted to estimate the mortality of coho and chinook during their ocean lives (Shapovalov and Taft, 1954, Parker and Kirkness 1956, Ricker 1976, Fraser et al. 1983). Sandercock and Healey (1991) have attempted to summarize the results of such studies for coho and chinook stocks, respectively. However, due to the variability in both the methods and the results of such studies, it is extremely difficult to establish a generally representative value for mortality rates of either species. To further complicate matters, almost all of the existing studies report an estimate of either overall smolt to adult mortality, or an average yearly mortality rate during ocean residence. It is generally held that such average marine mortality rates overestimate the actual mortality of adults, and underestimate that of smolts (McGurk 1996). Other than several suggestions that mortalities are probably much higher than average during early ocean residences (Shapovalov and Taft 1954, Parker 1962, Henry 1978, Healey 1991), very few studies have attempted to actually estimate a value for the mortality rate of coho and chinook smolts during their first six months in the ocean.

Mathews and Buckley (1976), working with coho in the Puget sound produced one of the few attempts at estimating mortality for coho in their first six months at sea. Using mark and recovery methodology, they estimated that only 13% of coho smolts survive their first six months in the ocean. This translates into an 87% mortality rate.

Converting this to a daily instantaneous mortality rate to be used in the bioenergetics model for coho smolts produced a value of 0.0113.

In the case of chinook smolts, no such study was available to provide an estimate of early ocean mortality. In fact, it is believed that no past studies have provided direct estimates for the marine survival rate of chinook stocks (Bradford 1995). In a summary of several studies producing estimates of annual mortality, Healey (1991) suggested that over their ocean life, chinook probably suffer a yearly mortality of 20%. However, this estimate was intended to represent an average of ocean going chinook of all ages. As stated above, such averages are known to underestimate smolt mortality (McGurk 1996). Also, the corresponding estimate derived for the coho mortality (above) was much higher, and it was suspected that the true chinook value would be somewhat closer to the coho estimate. Therefore it was assumed that the mortality rate in the first six months of life would be much higher than 20%. Thus, this value was adjusted upward to 67%. This was chosen as a reasonable compromise using the somewhat scant information available. This mortality rate translated into a daily instantaneous mortality rate of 0.00616.

### **Modelling Procedure**

Once I had specified all of the necessary parameter values, I conducted a set of modelling runs. The first step in this procedure was to divide the smolts entering the strait into cohorts. This was necessary since the values produced by the VPA estimated total smolt entries into the Strait for a given year. While the majority of these smolts enter the Strait early in late spring or early summer, they do not all enter the Strait at the same time. Healey (1980) found that most coho smolts enter the Strait in May and June. In the case of chinook smolts, he found that they also started to show up in the Strait in May.

Therefore, in order to spread out the impact of smolts on their food resources, and more realistically model the natural system, the total numbers of smolts for each population were split into three seasonal cohorts. The first and third cohorts were both 1/4 of the total estimated smolt populations. The middle cohort was the largest, representing the median entry date of smolts. It was composed of the remaining 1/2 of the total smolt population. The entry timing of these cohorts to the modelled population was spread out over three months, starting in May.

Thus, the program modelled a situation in which 1/4 of the smolts entered the Strait at the beginning of May, 1/2 at the beginning of June, and the remaining 1/4 at the beginning of July. While this is still an obviously artificial representation, it was assumed that this would spread the impact on the food supply out enough to reasonably model prey consumption in the Strait. Any misrepresentation would have been inconsequential later in the summer, since after July all the smolts are present and feeding in both the model and the actual Georgia Strait.

As already noted, all modelling runs were performed for two population sizes of both species. The smaller population represented a lower boundary estimate on the number of smolts entering the Strait each year, and therefore a lower estimate of the impact on food resources. The larger population was the upper boundary estimate, modelling a higher impact on food resources. Therefore, these estimates define a probable range of smolt numbers and their resulting impact on prey populations. It should be noted that this range is produced from a very conservative VPA procedure. This means that it is probable that the higher end is closer to the true case than is the lower end.

#### **Fitting P-values**

The first modelling run to be performed was termed a "P-fit run - fit to end weight" in the bioenergetics model. The purpose of this run is to determine a P-value for the fish. This value represents the proportion of the maximum ration the average individual fish has consumed. Maximum physiological feeding rates are determined by water temperature and the size of the fish. Thus, a P-value of less than 1 (i.e. 100% of the maximum rate) represents some kind of ecological constraint on feeding, such as prey availability, competition, predator avoidance, disease, etc. (Hewett and Johnson, 1992).

By employing the user-defined start and end weights, the computer determines the P-value that fits the observed growth. The model does this by starting with an estimated P-value (also user-defined) and performing a bioenergetics run to determine the resulting growth of fish feeding at that P-value. It then compares this growth with the observed growth. If the difference is more than 0.05%, the computer adjusts the P-value, and does a new bioenergetics run. It repeats the process until the P-value produces results that fit the observed growth within

0.05%. As P-values are determined for each cohort, the user is given the option of whether or not to replace his/her original estimate with the calculated P-value. In all cases, I accepted the calculated P-values as the best estimates.

### **Bioenergetics run**

The final step in the bioenergetics modelling process was to do the actual bioenergetics run. The run option chosen assumed a constant P-value. The model was set to simulate growth for the first six months of ocean life for both species of smolts. This time interval was chosen to represent the smolt stage of the life cycle based on feeding regimes. From my data, by late summer the smolts could be seen to be moving into an adult feeding regime, where the importance of fish and larger decapods overshadowed other prey items. Healey (1980) showed that young chinook were consistently present in the Strait throughout the six months from May to October. Presumably, after this period the majority have matured enough to migrate out to deeper water, and to adopt an adult, ocean-going lifestyle. In the same project, Healey studied young coho during their first six months in the Strait. Therefore, it was assumed that modelling the first six months of marine life realistically simulated the amount of time young salmon spend in the Georgia Strait.

Once the simulation was started, the model continued to track the smolt populations from the time they entered the strait until the end of October. The main output of this kind of bioenergetics run is the calculation of the amount of food consumption necessary to produce observed growth rates. Given that the bioenergetics model had time-series estimates of the proportion of each prey type in the smolt diets, the calculated total food requirements were apportioned to prey items. Thus, model outputs include both individual and population cumulative consumptions of all the prey types.

In addition to consumption calculations, the model provides daily calculations of many other interesting and potentially useful parameters. These include rates of growth, consumption, excretion, egestion and respiration. Also included are population parameters, including number, biomass, mortality, and energy density.

From this large amount of information, it is possible to perform simple calculations to extract many other details. However, the main thrust of the current study was to produce time series estimates of prey consumptions. Therefore, the cumulative estimates were imported into a spreadsheet program, where they were converted to daily

estimates by subtracting each cumulative value from that preceding it. Hence, the final output of the bioenergetics modelling process was four sets of time series data. For both species, a time series of the daily consumption of the various prey items was produced for the large and small population estimates. The values for both species were then summed, to produce an overall estimate of the total impact of chinook and coho smolts on their prey in the Georgia Strait (Figure 11). This impact is expressed in calories/cubic metre/day, using a value of 6300 km<sup>2</sup> as the surface area of the Strait (Thomson, 1981).

#### **2.4.2. Discussion of Results**

##### **P-fit runs - fit to end weight**

As was stated earlier, the first step in the bioenergetics modelling procedure is to determine P-values for the population being modelled, based on observed growth. These values provide an estimate of the feeding intensity of the population. An estimate of 1.0 means that the fish are feeding at their physiological maximum rate, as determined by water temperature and fish size. Any estimate less than 1.0 suggests that there is some sort of environmental constraint on the feeding of the population. Such constraints might take the form of reduced prey availability, increased competition, increased predator avoidance by the prey, or diseases in the predator population (Hewett and Johnson 1992).

For modelled populations of both species, the P-values were considerably less than 1. In fact, for the chinook population, the computer estimated P-value was 0.40. In other words, the bioenergetics model calculated that the chinook needed to feed at only 40% of their maximum rate to achieve the observed growth. Coho rates were slightly higher, with the model calculating a P-value of 0.5. This suggests that coho were feeding at half of their physiological maximum to attain the observed growth.

These results highlight the fact that the observed growth rates are not as high as they could be if the fish were feeding more intensely. Thus, there appears to be some factor constraining the feeding levels. Since the data used to estimate growth rates were obtained over several years, it is unlikely that a newly developed predator avoidance mechanism by the prey was in operation. Therefore, the most likely constraints producing these lower than maximum growth rates are either reduced prey availability or increased competition. These mechanisms are by

no means mutually exclusive, and the presence of one would increase the chances of the other occurring. The low P-values suggest that both may have been in effect at the time the growth data were collected.

However, a possible objection to this conclusion may arise when one examines the dates at which these data were collected. The fish that Healey used to infer growth rates were collected during several years. The earliest trawls were undertaken in the summers of 1966-1969. Later collections were made around the Strait in the summer months of 1972 to 1977 (Healey, 1980).

These collection years span the inception and early production years of SEP hatcheries, which are thought to be the most likely cause of increased competition and reduced prey availability for coho and chinook in the Strait. During these years, SEP releases of smolts into the Strait were relatively small, and just beginning to increase to the higher current levels. Therefore, one might suggest that the results of such competition should not have become manifest in the observed growth rates so early in SEP's lifetime. One would expect such results to have become apparent more recently, as SEP releases have reached even higher levels.

In an attempt to examine P-values as they relate to a more recent investigation, growth rates of the fish that were used in the stomach content survey were examined. Since these fish were caught in 1993, they were assumed to represent the current growth patterns in the Strait. Unfortunately, they represent a small sample size relative to Healey's data. They also were caught during a shorter period, in the middle of the summer. Both these facts serve to somewhat reduce their value in inferring growth rates of smolts over the six months from May to October. Nevertheless, P-values were produced for them.

In the case of the chinook, the growth rate calculated for my samples was somewhat higher than that which Healey produced. Where he saw an average growth rate of 0.8 mm/day over the first six months in the ocean, my samples displayed a growth rate of 0.96 mm/day over the middle summer months. Using this growth rate instead of Healey's, the model produces a P-value of 0.46, compared to a value of 0.40. The fact that this is still a low proportion of maximum physiological feeding rate suggests that, in the case of chinook, some ecological factor is indeed suppressing the feeding rate. Thus, this may be taken as further evidence of competition causing reduced prey availability to chinook in the Strait.

However, in the case of the coho smolts, my growth data do not support the same conclusion. From the fish caught in my study, the average daily growth appears to be 1.6 mm/day, which is a 60% increase over Healey's suggested 1mm/day. Using this increased growth in the bioenergetics model, the calculated P-value becomes 0.8, as opposed to 0.5. This suggests that coho are feeding at 80% of their physiological maximum in order to achieve the observed growth. This relatively high value does not support the assertion that ecological impacts are reducing the feeding ability of smolts in the Strait.

Another problem in trying to interpret the observed P-values was one of scale. While it was readily apparent that the calculated P-values were low relative to the maximum feeding rates, it was not readily discernible where they fell in the overall range of normal P-values at which the fish would be feeding. In order to rectify this situation, minimum P-values were calculated. These were defined as P-values at which no net gain in weight was experienced. In other words, they represent maintenance P-values, where the start and end weights for the modelling period are the same. For coho, the calculated maintenance P-value was 22% of the maximum feeding rate. For chinook, the value was 18%.

These low values suggest that the fish require relatively little food to maintain the same weight. Thus, there is a large range of P-values over which growth can be realized. At the same time, they suggest a scale for normal ranges of P-values for growing fish. If the maintenance values are taken to be the minimum boundary of this scale, and the physiological maximum is taken to be the upper boundary, it becomes readily apparent that the P-values calculated in the bioenergetics runs do in fact fall in the lower half of the range of growing fish.

Because of the variability in the calculated P-values, it is difficult to draw any firm conclusion from them. What does appear to be clear is that chinook are feeding at a low proportion of their maximum capability, which could be due in part to competition. Coho do not appear to be affected to the same extent, although using growth rates from a large sampling program, there is some evidence of low feeding rates. Once again, because Healey's values were drawn from a larger data set which covered a longer period, they were the ones that were used to produce the P-values for the main bioenergetics modelling runs.

It should be noted that the assumption of constant P-values was implicit in the modelling runs performed. Obviously, this is an oversimplification. In reality, smolts would be expected to feed at different proportions of

their maximum rate every day, in response to changes in the food supply they encountered. In fact, it is possible to model shorter time intervals with different P-values using the Fish Bioenergetics program. However, in order to do this, it is necessary to have weight data for shorter time intervals. Since the weight data used were inferred from growth patterns averaged over six months, I felt it was best to average the P-values over the same period. This simplification probably did not have much impact on the final result. In studies that have used both constant P-values, and multiple P-values split over shorter time intervals, the final estimates of total consumption have usually been similar (Hewett and Johnson, 1992).

#### **Total food consumption pattern**

Given the idealized feeding patterns specified for the bioenergetics run, the patterns of prey consumption that were produced are not surprising (Figure 11). The individual curves for each prey item are shaped by smolt entries to the Strait, timing of food preferences, and mortality reducing feeding populations. For example, copepods were a main prey item for both species at the beginning of the modelling runs. The rapid initial increase in copepod consumption is due to increasing numbers of fish entering the Strait, and their individually increasing consumption demands as they grow. Later, copepod consumption drops off as the smolts switch to larger prey items. Some of this decrease is also due to mortality reducing smolt numbers.

Much the same pattern is evident for both terrestrial insects and amphipods. The differences seen are due to the different timing of prey use suggested by the feeding regime (Figure 6). However, in the cases of decapod larvae and fish larvae, no major decreases are seen in their consumptions. This is because these items represent the adult feeding habits, in which other fish, euphausiids, and some crab larvae make up most of the diet. Therefore the fish continued to eat them beyond the end of the six month modelling run. Nevertheless, near the end of the run it can be seen that modelled predator mortality reduced the impact on decapod larvae to a certain degree. For both species, early concentrations on the smaller food items (insects and copepods) are replaced by the larger amphipods, decapods, and fish larvae.

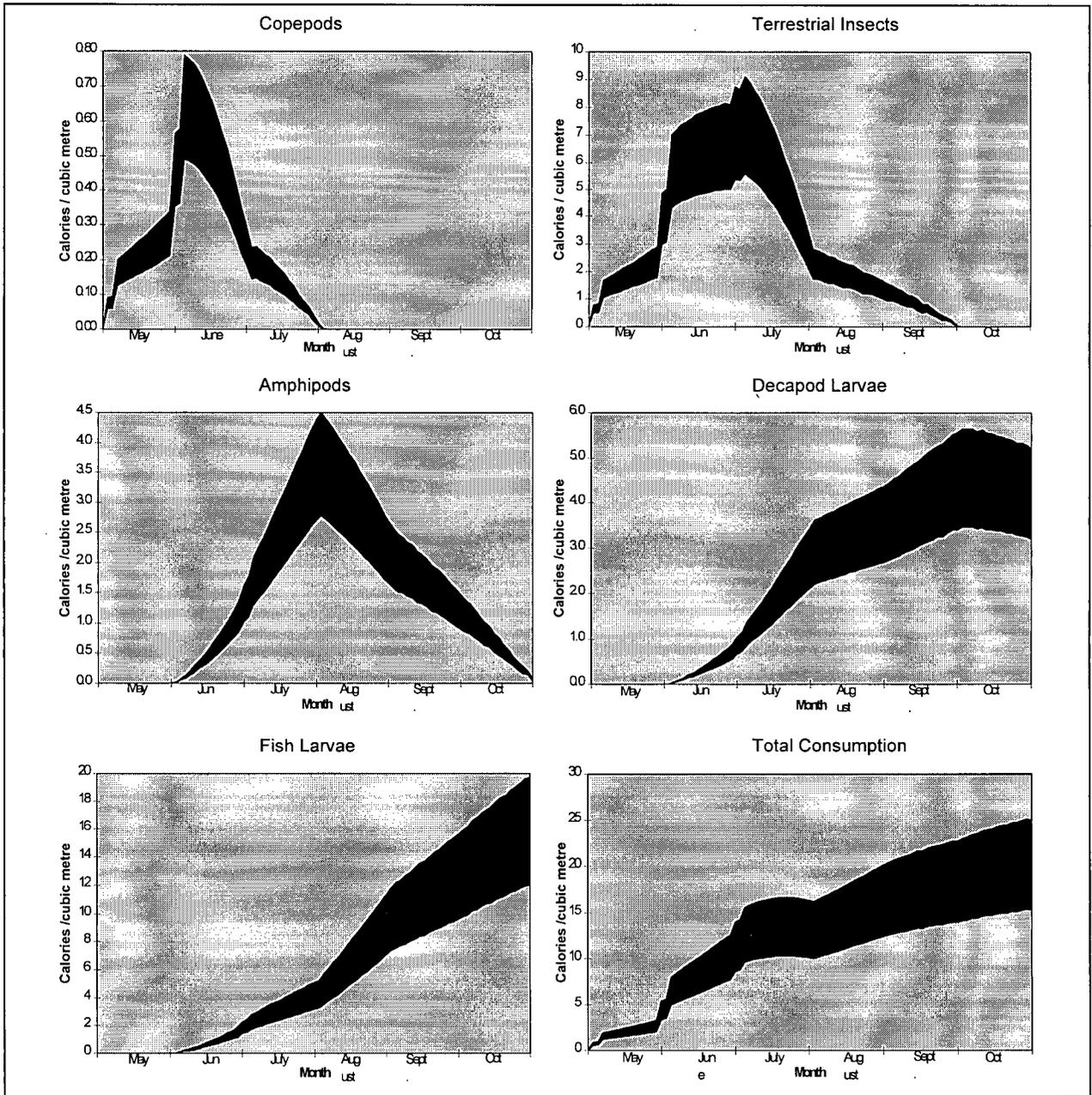
As was expected, the main differences between the small and large populations were in the amounts of each prey item eaten. Obviously, the larger populations ate significantly greater amounts overall than the smaller populations. Other than this, however, the relative patterns of prey item consumption were almost identical.

The fact that the smolts were modelled in separate cohorts is readily apparent from the consumption results. Particularly evident is the entrance of the large second cohort. This group of fish was modelled as entering the Strait after the first month, when fish were still concentrating on insects and copepods. Thus, a corresponding increase in the consumption of these prey items is seen. The entrance of the third cohort is less apparent. This is due to two factors. At the time of their entry, all five of the diet items are being consumed. Thus the impact of this new group of fish is spread out over prey types, and does not show a large impact on any single group. Also, this third cohort is a smaller one. It is half the size of the second cohort, so does not carry the same numerical impact.

Quantitatively, the overall results of the bioenergetics modelling are five sets of ranges. These ranges define the estimated total amounts consumed by both species of five separate prey types. The peak consumption of each prey type falls at a time when its use was specified to be highest by the idealized feeding patterns, by patterns of cohort entry into the Strait, and by assumed mortality losses over the summer.

For copepods, the highest consumption occurred in early June, when fish were still concentrating on smaller prey items. The range of consumption is estimated to be somewhere between 0.3 and 0.49 calories per cubic metre of the Strait surface per day. Terrestrial insects were the next prey item to peak. The highest consumption rates occurred near the beginning of July. The estimated range was 3.63 calories per cubic metre per day on the lower end, and 5.76 calories per cubic metre per day on the upper end. Amphipods, representing groups of smaller crustaceans, were consumed at the highest level at the beginning of August. The estimated amount of this peak is somewhere between 1.73 and 2.77 calories per cubic metre per day.

Figure 11. Range of consumption estimates for major prey items (in calories/cubic metre/day). Impacts of coho and chinook have been combined to show total potential exploitation of food supplies. Lower borders indicate small population consumption estimates, and upper borders indicate large population estimates.



Consumption of decapod crustaceans and fish larvae peaked toward the end of the modelling period. Decapod consumption was greatest in early October, with rates from 2.19 to 3.48 calories/m<sup>3</sup>/per day. Finally, fish consumption was still increasing at the end of the modelled period, reflecting continued predator growth, and

increasing piscivory. At the end of October, estimated fish consumption was between 7.73 and 12.1 calories/m<sup>3</sup>/day.

From these results, two important observations can be made. Firstly, the estimated amounts of prey eaten suggest that the two most energetically important food items are fish and terrestrial insects. For fish, this result was due to the fact that coho and chinook were modelled as being intensely piscivorous toward the end of the modelling run. Because this is also the time when the juvenile fish are at their largest, this means that large amounts of fish are being eaten. When this is combined with the relatively high energy density of fish (1900 cal/gram for clupeoids, Cummins and Wuycheck 1971) the net result is that, as coho and chinook enter their adult feeding phase, they derive large amounts of energy from eating other fish.

More surprising is the energetic importance of terrestrial insects in the diets. During the early summer, the model estimates that insects are the single most important food source. This is partly a result of a very high energy density (2300 cal/gram wet weight, Cummins and Wuycheck 1971). However, it is also due to the large amounts of insects that were seen to be consumed, particularly in my samples from 1993. This is surprising in light of the fact that insects would be expected to be a relatively ephemeral food source. They are probably supplied only at the surface, and only in times of strong offshore winds that blow them out to sea (Brodeur 1989).

The rest of the bioenergetics results were not unexpected, given the idealized feeding pattern that was used. Copepods contributed less in terms of relative energy supply than they did in terms of overall weight of food eaten, due to their low energy density (550 cal/gram wet weight). Amphipods and decapods, representing small and large classes of crustaceans, were important sources of food energy. Large crustaceans in particular become important for adult fish, as euphausiids make up a very large percentage of their diet.

### **Model Sensitivity and Limitations**

Having estimated the amounts and timing of prey consumptions, it is important to understand how precise they might be. Bioenergetics modelling is generally performed to achieve one of two goals. Estimates of growth from observed consumptions can be obtained. Alternatively, estimates of consumption from growth data can be produced, as was done in this study. The second type of estimation has been shown to be the more precise of the

two (Kitchell et al. 1977). Bartell et al. (1986) confirmed this assertion. They found that the bioenergetics model was very sensitive to variations in P-values. Thus constraining P-values to fit observed growth data improved the overall performance of the model. Most applications of bioenergetics modelling have estimated consumption from known growth parameters, as this also limits the effects of errors in temperature cycles, bioenergetics functions, and other necessary parameters (Hewett and Johnson 1992).

### **Activity**

Using the Stewart model, activity is calculated as a constant times resting metabolism. The integer multiplier ranges from 1 to 2, depending on the general activity level of the fish, as well as the actual metabolic level represented by the weight dependant swimming speed function (i.e. basal, resting or active metabolism). Since the development of this activity model by Stewart, more recent work has criticized this approach. Depending on fish species, age, water temperature and other parameters, some studies have shown that the correct integer multiplier probably ranges more broadly, from 1.5 to 4. Typically, the Stewart model underestimates activity (Boisclair et al. 1989). However, more recent work using  $^{137}\text{Cs}$ -labelled radiotracers has shown that for immature fish this discrepancy doesn't exist (Rowan et al. 1996). In fact, for immature fish, they found excellent agreement between Hewett and Johnson's activities using the conventional bioenergetics approach and their own. This suggests that the integer multipliers I used to estimate activity levels were probably at least in an appropriate range for my fish.

However, the 6-month life history that was modelled for my fish includes a rapid niche-shift from feeding on small zooplankton and insects to feeding on larger, faster moving fish. It is probable that, in reality, such a shift entails a significant increase in the fishes' activity levels. A linear increase in activity would require an exponential increase in consumption rates to achieve constant growth under constant temperatures (Hinch 1996). Therefore, by not including this activity change in my model, it is possible that I have underestimated the overall consumption levels necessary to achieve the observed growth.

This possible underestimation has some interesting implications for my results. If the model runs were repeated using higher activity estimates, then the estimates of overall metabolic rates would be increased. This

means that the fish would need to eat more in order to achieve the observed growth. Thus, the calculated P-values would be higher, since the fish would need to feed at a higher proportion of their physiologic maximum ability. This would serve to bring my P-values into closer approximation with those found in other studies modelling similar growth trajectories under similar temperatures (Brodeur et al. 1992).

However, by increasing activities and, as a result, increasing consumption rates, my eventual comparison of overall consumptions to estimated abundances would be more likely to show a carrying capacity limit. My policy throughout the bioenergetics modelling procedure was to err on the conservative side when alternative choices of parameters presented themselves. In this way, variability introduced by parameters with a greater degree of uncertainty was less likely to overestimate total consumption rates, and end up producing a false positive result for my carrying capacity estimation. Thus, in this case the lower activities provided by the "canned" swimming speed function were used. This is hoped to have produced the most conservative possible estimates of total consumption.

#### **Growth and Fish Size**

Because the growth observations and equations were produced using large sample sizes over an extended period (Healey 1980), I am confident that they provide a reasonable assessment of normal growth patterns. The only possible difficulty with them is that they are not recent data. Therefore, they do not necessarily model the current growth patterns being experienced by coho and chinook in the Strait. Ideally, in order to perform a better bioenergetics analysis, more recent data are necessary. However, the fact that the data used were gathered over several years should help to damp out minor variations in growth rates.

Another potential source of error in the bioenergetics model is related to fish size. The parameters used in the physiological modelling equations were derived using adult fish. However, the fish I attempted to model in the current study were young-of-the-year smolts. Modelling younger fish using adult parameters can be a source of bias, but it is usually only significant for very small fish. Adult fish parameters are thought to work well for any fish over 10 grams, and reasonably well for fish between 1 and 10 grams; it is only for fish below 1 gram that parameter modifications become mandatory (Hewett and Johnson 1992). In the current study, the starting weight

used for coho was 11.2 grams. Therefore, the adult parameters should have modelled them with sufficient accuracy. In the case of the chinook, start weight was 4.01 grams. Thus, the early season results for chinook may have some error introduced due to inappropriate physiological parameters. However, this source of error should have been low by the end of the first month of ocean life, after which chinook sizes were greater than 10 grams.

### **Population Size**

Another potential limitation of the bioenergetics modelling procedure comes from attempting to extrapolate individual fish results to the population level. The modelling procedure is essentially a single fish operation, dealing with physiology at an individual level. Population level results are produced by treating this individual as an average fish, and multiplying the results by the population size, which is computed using the initial population sizes and the mortality rates which are supplied as external parameters. However, estimates of population sizes and mortalities often have large confidence limits, as high as 50% or more (Hewett and Johnson 1992). I experienced problems in estimating both of these parameters in the current study.

Good estimates of mortality rates proved particularly difficult to find. It was because of the lack of this information that a normal VPA procedure was not performed. Instead, my modified VPA procedure substituted "representation coefficients" in place of juvenile to adult mortality rates. By using this modified VPA procedure, estimates of population sizes were produced. I am fairly confident that the range of estimates produced is a reasonable representation. This confidence is increased by the knowledge that the estimates are as conservative as possible, so that any error in them is likely to be on the low side of the true case.

Unfortunately, the representation coefficients were of no use in estimating the seasonal abundance declines over the first six months of ocean life which were necessary for the bioenergetics model. Therefore, for this period the best estimates from past studies were used. The variation in these estimates is quite high, and there is very little information on the mortality of chinook and coho during their first six months at sea. The lack of this information makes it very difficult to produce reliable population level estimates from a bioenergetics model. Any future attempts at similar procedures should involve a tag and recovery program to estimate early ocean mortality for salmon smolts. Alternatively, it may be possible to employ recently derived allometric relationships of mortality for

Pacific salmon (McGurk 1996). With respect to the current study, I used mortality rates that were among the highest estimated by past studies. However, more recently published information suggests that the chinook estimates should probably have been higher than those used for coho (Bradford 1995). Nevertheless, it is hoped that using relatively high early ocean mortality estimates for both species produced conservative estimates of overall population consumptions, so that any potential carrying capacity limit that might be seen is not the result of overestimating smolt numbers in the Strait.

### **Energy density**

In using the bioenergetics model, I assumed that energy densities of the prey were consistent for the duration of their importance as a food item. At the same time, variability in the predator energy densities was modelled as a function of their weight. Obviously, it is more accurate to assume that energy densities of organisms vary by season and by size of the organism. However, using average densities tends to give fairly accurate estimates for longer term modelling runs. Also, results are less affected by errors in energy density than by errors in population size and mortality rates (Hewett and Johnson 1992). Therefore, the constant energy density assumption for the prey items is assumed to introduce little, if any, error into the results.

### **Timing of smolt entries**

Finally, there are undoubtedly estimation errors due to assumptions about the timing of smolt entries to the Strait. After estimating the total numbers of smolts in the Strait, I realized that all of the smolts would not impact the prey resources as a single group. Therefore, in order to diffuse their impact, they were modelled as three separate groups, entering the Strait in three separate months. The largest of the three groups was timed to enter the Strait closest to the mean entry dates of the smolts.

In reality, the natural situation is much more complex than this. Smolts are constantly entering the Strait from different river systems throughout the early summer. Therefore, instead of three large groups of smolts entering, there are actually hundreds or thousands of smaller groups that combine to produce the overall smolt

population. However, it was impossible for the model to handle this degree of complexity. The number of cohorts that could be simulated in a single modelling run was much too limited to model smolt entries as a smooth curve.

Thus, it is possible that substantial error in the timing of predator impacts on prey populations was introduced. Nevertheless, the overall numbers of smolts used is assumed to be reasonably accurate. Therefore, the magnitude of prey consumptions should represent realistic values that would be achieved at some point in the summer. Also, it is known that most smolts enter the Strait in the spring and early summer months (Healey 1980). This means that, in the later months, the entire smolt population would be impacting prey supplies in unison. Thus, later in the summer, timing of entries into the Strait is probably not of much importance.

#### **Confidence in model estimates**

Given all these limitations, one may question whether or not any confidence can be placed in model estimates of consumption. However, it should be remembered that model and field estimates are both only as good as the data that goes into them. Moreover, both are limited by different sets of assumptions. In fact, model estimates may actually be more accurate than field estimates when unknown sources of error exist in field data (Hewett and Johnson 1992). By producing estimates that are boundaries on a range, I hope to have defined a reasonable "ballpark" of consumption estimates. Once again, it should be pointed out that, if anything, these estimates are probably conservative. If substantial errors do exist, the true values of prey consumptions in the Strait are probably higher than the estimates produced from the bioenergetics model.

Overall, I have the most confidence in the magnitude of the consumption estimates. The main source of error in these estimates comes from insufficient mortality data for chinook and coho in their early ocean residence. I place less confidence in the estimated timing of prey use. These estimates are based on the idealized feeding pattern, and the timing of smolt entries into the Strait. The idealized feeding pattern depends heavily on my stomach content data, which, while detailed, covered a relatively short period of time. The timing of smolt entries into the Strait, as mentioned above, is admittedly artificial, due to limitations in modelling the complex series of real smolt entries into the Georgia Strait.

## 2.5. FOOD AVAILABILITY STUDY

Thus far in my investigation of potential food limitation, I have produced estimates of salmon abundances and prey consumption rates. The final step is to compare these consumptions to reasonable estimates of the prey available to be consumed. Unfortunately, zooplankton samples were not collected concurrently with salmonids during the 1993 sampling process. Therefore, I was dependant on historical data to try and gain knowledge about prey abundances in the Georgia Strait.

There have been several attempts to quantify the abundance of most of the zooplankton that appear as prey types in juvenile salmon stomachs in the Georgia Strait (Brown et al. 1987, St. John et al. 1992, and Clifford et al. 1989 and Clifford et al. 1991). Zooplankton abundances are reported as numbers of organisms per cubic metre of water in these studies. Combining data from these sources, I produced estimates of the average numerical abundances of the relevant salmonid prey species.

However, a difficulty arose when I attempted to convert these numerical abundances to biomass, and thereby caloric abundances. Because the average weights of the organisms counted were not reported in the historical collections, it was impossible to derive biomasses from them.. Therefore, it was necessary to refer to studies of abundances outside of the Georgia Strait in order to obtain weight data.

Brodeur et al. (1992) report average Washington and Oregon Coast zooplankton abundances from 1981 as mean wet weights. These samples were taken in the summer, during the same months as the fish were sampled and modelled in the current study. Therefore, they were assumed to represent reasonable estimates of zooplankton sizes for the Georgia Strait, and were used as comparison values for the estimated consumption rates.

The only diet item whose abundance I could not estimate in this manner was terrestrial insects. None of the B.C. coastal zooplankton surveys included count or weight abundance estimates of terrestrial insects at sea. However, a few authors have attempted to quantify the density of terrestrial insects found at sea. Brodeur et al. (1987) counted mean abundances of terrestrial insects found along the Pacific coast, from California to Alaska. While they did not include mean weights of the insects, Bowden et al. (1976) estimated that a similar assemblage of insects found on the decks of ships in the North Sea had a mean weight of about 0.5 grams per individual (wet weight). Using this value, it was possible to calculate that Brodeur's samples represented a mean insect density of

0.034 cal/cubic metre along the Pacific Coast. In a similar study, Cheng (1975) estimated that the insect density in the central northern Pacific was about 0.145 cal/cubic metre. Interestingly, this value was higher than Brodeur's despite the fact that collections were made in the winter, and farther out to sea. One would expect this situation to produce relatively low insect densities. Another study on the Black Sea showed insect densities of 1.82 cal/cubic metre (Zaitsev 1970). The generally held view that the abundance of terrestrial insects at sea is highly variable depending on the season and the distance from land (Bowden et al. 1976) is supported by these three sets of observations. In the case of the Georgia Strait, it was assumed that the high abundances observed in the Black Sea would be the most representative, since both bodies of water have large areas of coastline to serve as a source of terrestrial insects.

Once abundance estimates had been produced and converted to calories per cubic metre, it was a simple matter to compare them with consumption estimates and arrive at an assessment of the daily percent use of prey. The estimated daily consumption rates were averaged over the modelling period. These were then compared to the average estimated abundances, to provide a representation of the degree of exploitation of available prey. The data are presented in Table 10.

Table 10. Prey consumption (cal/m<sup>3</sup>/day) vs. abundance estimates (cal/m<sup>3</sup>).

Item:	Consumption Estimates		Average Abundance Estimates*	Percent Exploitation	
	Lower Bound	Upper Bound		Lower Bound	Upper Bound
Insects	1.26	2.00	1.82	69%	110%
Copepods	0.06	0.10	8.64	1%	1%
Fish	2.84	4.52	63.32	4%	7%
Amphipods	0.65	1.04	14.68	4%	7%
Decapods	0.64	1.02	52.82	1%	2%
All Prey Types	5.45	8.68	141.28	4%	6%

\*from Brodeur et al. 1992

### 2.5.1. Discussion

On examining the percent use estimates, the most striking value is the high estimated exploitation of insects by the juvenile salmonids. The fact that the upper bound of this estimate exceeds 100% indicates that the supply of

insects is turning over rapidly within the feeding environment. There are several potential avenues of insect supply to the sea surface that could be responsible for this high rate of renewal.

Brodeur (1989) found that offshore winds could be responsible for supplying large numbers of insects to surface waters. Because the Georgia Strait is surrounded by large land masses and contains many chains of islands, there is no shortage of land area to supply terrestrial insects via such winds.

Large numbers of insects may also be supplied to feeding salmon in the Georgia Strait through other means. The large plume created by the Fraser River as it empties into the Strait is a dominant oceanographic feature. The plume has been shown to be an important feeding area for juvenile fish. Significantly higher densities of young salmon occur in the plume than in the main Strait. The increased numbers are believed to be due to aggregations of zooplankton, as well as a lower salinity environment which allows salmon smolts to acclimatize more slowly to a marine environment after they leave their freshwater habitat (St. John et al. 1992). This pattern of high salmon densities in the plume was borne out in the current study. Because of this, a majority of the stomach samples used to define the idealized feeding pattern in the bioenergetics model were obtained from fish that had been feeding in the plume.

Along with increased zooplankton densities, it is possible that these fish encountered higher than normal terrestrial insect densities. The Fraser River may act as a sort of "conveyor belt" of terrestrial insects, trapping them from the surrounding land as it runs its course, and emptying them into the Georgia Strait. Thus, the Strait, and especially the plume, might well have densities of terrestrial insects much higher than was found in the studies used to define the abundance estimate. Even if the standing stock of insects are being consumed at very high rates, it is possible that the supply is replenished very rapidly, as the Fraser continues to collect insects along its length and deliver them to the congregated fish at its mouth.

Despite the existence of potential errors in the calculation of insect consumption, the fact remains that, using the best information available, percentage rates of insect exploitation were estimated to be one to two orders of magnitude higher than any other prey item. Depending on turnover rates of insects at the surface, these values must be taken as a suggestion that the supply of insects to feeding salmonids could be limited. If such a limitation

exists, it probably occurs very early in the ocean residence of the salmonids, when they are still eating the same types of prey that they consumed in freshwater.

While the extremely high rates of insect consumption are worthy of note, a further species by species comparison of consumption rates to abundance estimates is probably not a useful exercise. This is true for two reasons. Firstly, the feeding regime used was meant to represent an idealized pattern. In order to create this regime, I included the food items that were the most important in present and past stomach content analyses of juvenile salmon. While these items are assumed to cover the majority of the fish diets, they do not include every potential prey item available. That is why prey items were represented by energy densities in the bioenergetics model. This allowed them to be used as representative organisms, that could characterize any organism of a similar size and biochemical makeup containing roughly the same number of calories per unit weight. For example, when I estimate that the fish consumed 1.02 calories of decapod crustaceans per metre<sup>3</sup> per day, this can be understood to mean that that much energy was derived from moderately large crustaceans, including decapods and other species such as euphausiids. Nevertheless, from the stomach content analyses it seems probable that most of this energy was indeed derived from decapods (at least early in the summer).

The other reason that a species to species comparison is probably not useful is that salmonids are known to be opportunistic feeders that will shift their predation efforts to the most readily available food items. This means that, as long as one food item is available, it is unlikely that dependence on another rare food item will cause a carrying capacity limit. If a limit does exist it would probably be a result of consumption rates that are high enough to significantly impact *all* the major food items in the salmonid's diet. Therefore, in investigating a potential carrying capacity limit, the most informative comparison is that of total energy consumption to total availability.

When compared with the extreme values estimated for insect use, the estimate of total average consumption as a percentage of the total average biomass (4% to 6% per day) seems low. However, other studies have estimated much lower overall consumption rates, such as 0.05 to 0.10% and 0.2 to 0.4% (Brodeur 1992, Peterson et al. 1982). Relative to these values, the current model suggests that juvenile salmonids are eating a very high proportion of the available food.

Several other factors support this perception of high overall consumption rates. The first is that juvenile chinook and coho do not represent the only demand on the zooplankton resources in the Georgia Strait. Many other fish species, including adult salmonids, occur in pelagic waters, and consume the same types of prey as juvenile coho and chinook (Brodeur et al. 1987). In fact, Brodeur and Percy (1992) showed that juvenile coho and chinook together represented an average of only 6.5% of the demand on pelagic nekton found along the Washington and Oregon Coast in May and June, 1981 through 1984. Other juvenile salmonids, including chum, pink and sockeye salmon, as well as steelhead and cutthroat trout compete with coho and chinook for many of the same prey items. Competition also occurs in the form of adult salmonids, macrozooplankton, and marine birds and mammals. If one were to include the consumption of zooplankton resources by these other predators, the result would be much higher overall daily rates of use than was estimated for juvenile coho and chinook alone. Thus, the fact that coho and chinook are estimated to consume between 4 and 6% of the available prey each day, while only making up about 7% of the total demand, may indicate that much higher levels of zooplankton consumption are occurring. This provides further evidence for potential food limitation.

It is incorrect, however, to consider zooplankton resources as a static supply. In reality, standing stocks do not accurately represent the potentially rapid production and recruitment of new biomass to the plankton population. This turnover can serve to augment the supply of zooplankters as they are impacted by predator species. Shannon and Field (1985) found turnover times of zooplankton in upwelling ecosystems to be on the order of 5 to 10 days. However, production rates may be much higher during the summer months, when growth and recruitment are at a maximum (Walters et al. 1978). Nevertheless, a quick calculation using conservative estimates shows that if juvenile coho and chinook are consuming 4% of the standing stock per day, and this represents 10% of the total demand, the standing stock would be exhausted in 2 to 3 days. Therefore in order to satisfy the consumption rates estimated by the bioenergetics model, turnover rates would have to be much less than 5 to 10 days. Thus, these estimates may provide further evidence of a potential carrying capacity limit.

It should be noted that the *average* daily consumption estimates were compared against zooplankton availability estimates to define prey exploitation rates. If I had used the *maximum* estimates of daily consumption, the exploitation rates would have been much higher than 4 to 6% per day. However, the timing of the maximum

rates of prey consumption was somewhat suspect. As already mentioned, the estimated timing of prey use depended on the idealized feeding pattern, and the timing of smolt entries into the Strait. Both of these were admittedly oversimplified. Therefore, it is unclear *when* during the summer the maximum rates of prey use would actually occur. This makes it difficult to compare these maximums against any specific estimates of zooplankton stocks. Nevertheless, it is important to realize that, at some point during the summer, prey exploitation rates would reach a much higher level than represented by the average rates. Thus, if a carrying capacity food limitation was to occur, it would probably be around such a time.

In considering the evidence supporting a potential carrying capacity limit in the Georgia Strait, it is important to remember that several factors limited the accuracy of my estimation procedure. For example, a major problem was encountered in trying to obtain abundance estimates of zooplankton in the Georgia Strait. Since the 1993 sampling cruises were only intended as a census of juvenile salmonids in the Strait, there was no concurrent sampling of zooplankton species. Therefore it was necessary to use historical studies to fill in this gap in knowledge. Unfortunately, the most applicable historical studies were done outside the Strait, in waters off the Washington and Oregon Coasts. Obviously these were less than ideal samples, as differences in environmental variables may produce different levels of zooplankton. In fact, Shenker (1988) found that substantial differences in species compositions may occur over relatively short distances. Therefore the Washington and Oregon coast samples may have been very poor indicators of prey composition and abundances in the Georgia Strait. Nevertheless, these were the best samples available for the current study. Ideally, if such a study were to be repeated, zooplankton samples would be taken in conjunction with fish sampling efforts, and the stomach contents then compared directly to the zooplankton in the same area.

However, even this would not eliminate the sources of error associated with potential sampling biases due to prey patchiness. Most zooplankton species occur in patches of relatively high density, interspersed with areas relatively free of that species. Since salmon can focus their feeding in these high density patches, they may in fact see relative densities of zooplankton that are much higher than the densities sampled in vertical net hauls, or bongo net tows. Harrison et al. (1983) felt that zooplankton densities using vertical net hauls may have been as much as an

order of magnitude underestimation of patch densities. If this were to prove true of the zooplankton densities in the current study, then the case for a food imposed carrying capacity limit would be much weaker.

The plankton sampling method may have been insufficient in other ways, as well. Brodeur (1989), who produced the neuston samples used in the current study, felt that the sampling gear may have been inadequate in collecting certain of the prey species. Juvenile fish, for example, may have been mobile enough to avoid being caught in the nets, and therefore would not be caught in proportion to their abundance. Also, many invertebrate zooplankton species are known to undergo extensive diel vertical migrations, often coming to the surface only at night. Therefore, plankton samples taken in the day might largely underestimate the actual abundance of these prey species.

Other potential sources of error lie in the feeding regime construction and in the VPA estimation of smolt numbers. However, the problems in these procedures were anticipated, and any assumptions that had to be made were kept as conservative as possible. For example, there is some possibility that major food items exist in the Strait that were not accounted for in this study. If this were the case, the impact of salmon smolts on potential food sources might be much less than was estimated. However, in order to minimize this source of error, nearly 600 stomachs were analyzed in the current study, and this information was combined with major historical data sets to try and get as clear a picture as possible of juvenile salmon feeding habits. Nevertheless, late in the summer when the smolts are switching from a juvenile to an adult diet, the feeding regime became somewhat unpredictable. To avoid problems associated with this ambiguity, the bioenergetics results were only considered up until the end of August. Any estimated limitation due to low zooplankton abundances after this time would probably be invalid, since the fish would be more capable of supplementing their diets with euphausiids or other fish species.

Finally, it should be noted that several assumptions were necessary to perform the VPA procedure, and produce estimates of smolt numbers entering the Strait. In all cases, I attempted to err on the conservative side, so that my estimates of smolt numbers would be, if anything, on the low side. Nevertheless, any future attempts at performing a VPA to estimate smolt numbers entering the Strait would greatly benefit from better early mortality estimates for juvenile salmonids.

## 2.6. SUMMARY

Overall, the food, VPA and bioenergetics analysis support the hypothesis that food limitation may be the proximate cause of reduced coho and chinook survival in the Georgia Strait. This evidence is bolstered by the low P-values, indicating reduced rates of feeding, estimated by the bioenergetics model. If such a limitation exists, it probably occurs between May and September, before euphausiids and fish become the main components of the salmonid's diet.

Unfortunately, several sources of error serve to limit the degree of confidence that can be placed in these results. The primary problem lies with uncertainty surrounding the zooplankton abundance estimates. Also, there is some possibility that the feeding pattern may be more variable than it appears from this study.

To reduce the influence of these sources of error, future research using this approach should focus on replicating feeding studies over several summers, in order to get a more accurate picture of the important elements in the salmonid diet, and the degree of temporal variation that exists. Also, zooplankton sampling should be done concurrently so that the comparison of what is being eaten to what is available is more accurate. Finally, it would be very useful to incorporate a mark/recapture study of both wild and hatchery smolts that allowed a better estimation of early ocean mortality rates.

**CHAPTER 3:**  
**METAGAME - A COMPUTER MODEL TO ASSIST IN DESIGNING A LARGE SCALE FISHERIES**  
**EXPERIMENT.**

**3.1. INTRODUCTION**

The direct feeding study described in Chapter 1 provides evidence that a food imposed carrying capacity might be limiting the production of coho and chinook salmon in the Georgia Strait. Unfortunately, there is much uncertainty about the parameters used to produce estimates of both salmon consumption and food availability. Nevertheless, having recognized these uncertainties, the results of Chapter 1 should be more than adequate to highlight the need for further study. The question then becomes, what form should future investigations take?

There are two main options that suggest themselves immediately upon considering the results of the direct feeding study. The first and most obvious is to carry out a more detailed study of the same kind, with improved estimates of the suspect parameters. Such a project would have to include mark/recapture work to more clearly estimate mortality rates of young salmon in the Strait. Also, appropriate sampling of the zooplankton stocks in the Strait would be necessary to more accurately gauge the availability of salmon food supplies. Finally, the time frame of the study would need to be extended, so that sampling of both salmon stomachs and zooplankton could be carried out over several summers. This would provide a better idea of the variability in resource use and availability. However, ultimately this approach would not prove anything. It would provide only a more precise model of the food limitation hypothesis, not a direct test of this hypothesis in terms of the link between food and marine survival rates.

It should be possible to carry out a very different kind of study that addresses a more specific question: has hatchery production caused the salmon populations in the Georgia Strait to reach a carrying capacity limit involving density dependence in marine survival rates? By phrasing the question in this manner, we remove the emphasis from the proximate cause of the limitation. In other words, it becomes unnecessary to investigate which ecological resource is directly responsible for imposing a constraint on population size. Instead, the focus is shifted to the

factor that is almost certainly responsible for failure of populations to increase in conjunction with enhancement, namely decreases in marine survival rate.

The obvious method of investigating the impact hatchery releases are having on Georgia Strait salmon populations is to perform an experimental manipulation of hatchery releases, and examine the impact of these manipulations on marine survival rate. Obviously, if such an experiment were to be successful, it would require large scale cooperation of hatchery and fisheries managers throughout the Strait. In order to achieve such cooperation, many questions about the details of the experiment would have to be answered before it was attempted. For example, how long would such an experiment take to show any conclusive results? And to what degree would releases need to be manipulated in order to measure density-dependant survival effects? Also, how definitive would the results of such an experiment be? Would they make future management decisions perfectly clear, or would some uncertainty still remain? All of these questions have far-reaching implications as to the usefulness and viability of such an experiment.

In an attempt to shed some light on these questions, a computer model of the coho and chinook stocks in the Georgia Strait was developed (Walters 1994). The "Coho and Chinook Hatchery Evaluation Game" simulates wild and hatchery populations, and the interactions between the two. It also allows the user to simulate different manipulations of the size of hatchery releases, every second year (the alternating year treatment structure allows "temporal blocking" to provide paired comparisons of high and low smolt density years). This provides information on what results may be expected if different stocking reduction protocols were attempted.

The model is built around the assumption that one of the four hypotheses mentioned in the general introduction is responsible for the decline in wild stocks and failing salmon catches in the Strait. These hypotheses are:

1. Over fishing.
2. Freshwater rearing habitat limitation.
3. Changing oceanographic conditions.
4. Marine carrying capacity.

For further explanation of these hypotheses, and the arguments for and against each of them, see the general introduction.

### **3.1.1. What the "Game" in the Metagame Program Does**

When a user starts a gaming session with the program, the first thing it does is to display information from 23 years of historical data. This information includes catches in the Georgia Strait, hatchery smolt releases, proportion of catches that were wild fish, and marine survival rates from CWT data. After the historical data has been produced, the game player has three main choices.

The player can choose to simulate one year at a time, and observe catch and population data on this basis. In simulating a year, the program simultaneously does three important things. First, it has already picked one of the four hypotheses at random. The user does not know which hypothesis has been picked. At the same time, the computer generates fake data for that year, by simulating the year according to the chosen hypothesis, and adding random variability. While this is going on, the program simulates all four of the hypotheses independently, using the current parameter settings and whatever information the player has entered. Then, the program uses a Bayesian assessment method (explained in section 3.2.1) to compare the observed (fake) data, to the simulated data predicted by each hypothesis. Using this comparison, the program generates a Bayes posterior probability for each hypothesis. After several years of play, informative management choices, such as hatchery release manipulations, will cause these probabilities to shift such that the "true" (prechosen) hypothesis becomes progressively more probable.

The player can also choose to carry out a simulation for a preset number of years. This is akin to deciding to apply a single experimental regime for multiple years. The program simulates this regime for multiple years. At the end of such a run, the hypothesis that was being used to generate the fake data is revealed to the user. This can then be compared to the Bayesian probability for that hypothesis to see how successful the manager would have been at deciding which hypothesis was true given the experiment that was run.

The final choice for the user is the most powerful of the three in evaluating how successful an experiment would be in discovering the true hypothesis. The user can choose to run an experiment for a given number of years,

as outlined above, but to do it *multiple times*. In other words, the user can simulate a situation in which many fisheries managers carried out the same experiment, at the same time, but independent of each other, as if they were on separate but identical worlds. Of course, the results of the experiments are not identical, since the model incorporates random variability in measurements and in survival rates. The user can then observe the outcomes of each of these experiments, to get an idea of how many of the experiments resulted in strong support (high posterior probability) for the correct hypothesis. This gives the user an estimate of what the odds of running a successful experiment might be, given a certain set of parameters and a certain length of time. In the parlance of the program, this procedure is called a *multiple run* or *multitrial*. In traditional statistical terms, a multitrial measures the "power" of a proposed experimental design.

It is important to explicitly state the question that the program attempts to answer with a multiple run. Since the program is written with a hatchery manager's interests in mind, the question that is being answered is not "How successful will a given experiment be at telling me which of the four hypotheses is the true one?" Instead, the question being addressed is "How successful will a given experiment be at telling me whether or not hypothesis 4 (marine carrying capacity) is true?" There is a subtle but important difference here. This is because the only hypothesis that suggests that the hatcheries are having an impact on salmon survival in the Georgia Strait is the carrying capacity hypothesis. Thus, this is the only hypothesis the hatcheries are in a position to test through an experimental reduction in stocking rates. In other words, a reduction in stocking rates will not alter the situation for hatchery managers in the Georgia Strait if one of the first three hypotheses is true. Therefore, the only insights that can be gained through such an experiment are:

1. Did the marine survival situation in the Strait change in response to our experiment? (Hypothesis 4 is true.)
2. Did the situation in the Strait not change in response to our experiment? (One of hypotheses 1 through 3 is true.)

This is not a problem for the program from a hatchery manager's perspective. While it might be nice to know what is really going on in the Strait to satisfy one's curiosity, the only really important question for the hatchery manager should be "Are my activities having a negative impact on the wild salmon in the Georgia Strait?" The Metagame is designed to help devise an experiment to answer that question.

## **3.2. MATERIALS AND METHODS**

### **3.2.1. The Bayesian Assessment Method**

The Bayesian assessment method is the statistical process that the program uses to calculate probabilities of each of the four hypotheses, given the "fake" data that are generated. This section outlines the general ideas behind this method, and how it works.

Bayes' theorem provides a way in which to combine three basic ingredients as a means for inference (Walters 1986). The necessary components are:

1. A set of models, or hypotheses about how a managed system will respond to manipulation. In the Metagame program, these are the four hypotheses discussed above, which are defined by parameters set in the program.
2. A set of historical observations of the system under consideration, that are incorporated into an historical "database" about the system. For the Metagame program, these observations are drawn from the "fake" data, generated by the program by using one of the four hypotheses chosen at random.
3. A set of "*prior probabilities*" that would be assigned to the alternative hypotheses in the absence of any specific data about the system being questioned. These prior probabilities are generated based on experience gained from observations of other, similar systems. There is often some disagreement about what level of probability to assign to each alternative hypothesis as a "prior". For example, there is evidence to suggest that the habitat limitation and over-fishing hypotheses are less likely than the oceanographic conditions or the marine carrying capacity hypothesis. If we could prove that this

was the case, it might be possible to arrive at conclusions about what was really going on in the Strait much faster by assigning lower prior probabilities to hypotheses 1 and 2. However, in order to avoid letting any unfair subjective bias colour the results obtained using the Metagame program, all four hypotheses are given equal probabilities at the start of each run, and the evaluation is made from this initial state. Assigning reasonable "uniform priors" in this way also provides the simplest computational option (Walters et al. 1994).

Once these ingredients are supplied, Bayes' theorem provides us with a means to contrast observations generated using each model against the actual data set. This comparison allows us to calculate a "*posterior probability*" that each hypothesis is true. The calculation involves two steps. First, the program computes the values that would be expected for each hypothesis if that hypothesis was true. Then the deviations of the simulated ("observed") data from the expected values are calculated for each model. These deviations, when combined with the variance in the simulated data, provide a means of estimating the likelihood of the "observations" given each alternative hypothesis.

Once the likelihood of the data has been calculated for each model, it is a simple matter to calculate the Bayes' posterior probability for each hypothesis. This calculation is simply the ratio of each estimated likelihood to the sum of the likelihoods over all the hypotheses. It is assumed in this calculation that equal prior probabilities were used (Walters 1994). The equation is as follows (Walters et al. 1994):

$$\text{(Posterior probability of the data given the hypothesis)} = \frac{\text{(Likelihood of the data given the hypothesis)}}{\text{(Sum of the likelihoods over all the hypotheses)}}$$

Thus, the Metagame program can assign a probability to each hypothesis after each year of a simulation. In general, the more information that is available to be compared, the more accurate the posterior probability will be. Therefore, the probabilities in successive years of a program run tend to point increasingly to one of the four hypotheses, until eventually its probability of being true is very high, while the probabilities of the other three hypotheses are low.

### 3.2.2. The Stock Production Model

The stock production model used in the program is one in which all the variable parameters are set by the user, and can be changed at any time. Throughout the production model, wild and hatchery fish are survived and recruited separately, and are combined only to produce total smolt and total catch numbers. The life history of the wild fish is modelled in two stages: firstly, this year's spawners to next year's smolts and, secondly, smolts to adults. Hatchery fish require only the second step, since the smolt numbers are calculated from hatchery releases.

The number of wild smolts is calculated from spawners by an equation of the Beverton-Holt form. Beverton-Holt type equations predict that recruitment will increase to an asymptote with increased spawning stock sizes (Walters 1986). The equation used in the Metagame is as follows:

$$\text{Wild Smolts} = \frac{[(S_{\text{max}}) \times (\text{Fec}) \times (\text{N wild spawners})] \times e^{\omega_1}}{1 + \frac{[(S_{\text{max}}) \times (\text{Fec}) \times (\text{N wild spawners})]}{\text{max smolts}}}$$

where:

$S_{\text{max}}$  = the maximum survival rate experienced by smolts.

$\text{Fec}$  = an expression of the fecundity of the spawners (i.e. how many eggs they lay).

$\text{N wild spawners}$  = the number of wild spawners.

$\text{max smolts}$  = the maximum number of smolts that can exist in the environment.

$e^{\omega_1}$  = a random normal variability effect.

Given this equation, the slope of the increasing part of the stock-recruitment curve is provided by  $(S_{\text{max}})(\text{Fec})$ . This expression is manipulated to help define the freshwater habitat deterioration hypothesis. For this hypothesis,  $S_{\text{max}}$  is lower than the other three; therefore, fewer smolts survive to adulthood. The asymptote of the curve is defined by the (max smolts) parameter value. Under the marine carrying capacity hypothesis, this value is reduced relative to the other hypotheses. Therefore, the number of smolts that can exist in the marine environment are limited under hypothesis 4.

To calculate the number of adult salmon derived from smolt populations the Metagame uses a simple relationship:

$$\text{Adults} = (\text{mean smolt to adult survival rate}) (\text{number of smolts})$$

The four hypotheses are differentiated from one another in the expression that is used to express mean survival rate (MSR).

For the overfishing and habitat depletion hypotheses, the MSR is expressed as a set base value that is altered yearly by a randomly generated variability effect. For the changing oceanographic conditions hypothesis, MSR is produced in the same manner, except that the variability effect is highly auto-correlated. This means that the variation in any given year is tied to that produced for the previous year. Therefore, changes in MSR occur slowly, over several years, as would be expected if climatic or other oceanographic conditions were producing the change.

For the carrying capacity hypothesis, MSR is calculated using a Beverton-Holt form equation, as follows:

$$\text{MSR} = \frac{[(\text{MSR max}) \times e^{w^4}]}{1 + \left[ \frac{(\text{total smolts}) \times (\text{MSR max})}{(\text{adult carrying capacity})} \right]}$$

where:

MSR max = the user defined maximum marine survival rate for hypothesis 4.

total smolts = wild + hatchery smolts.

adult carrying capacity = 1.5 million fish (as opposed to 10 million for the other hypotheses).

$e^{w^4}$  = an expression providing variability.

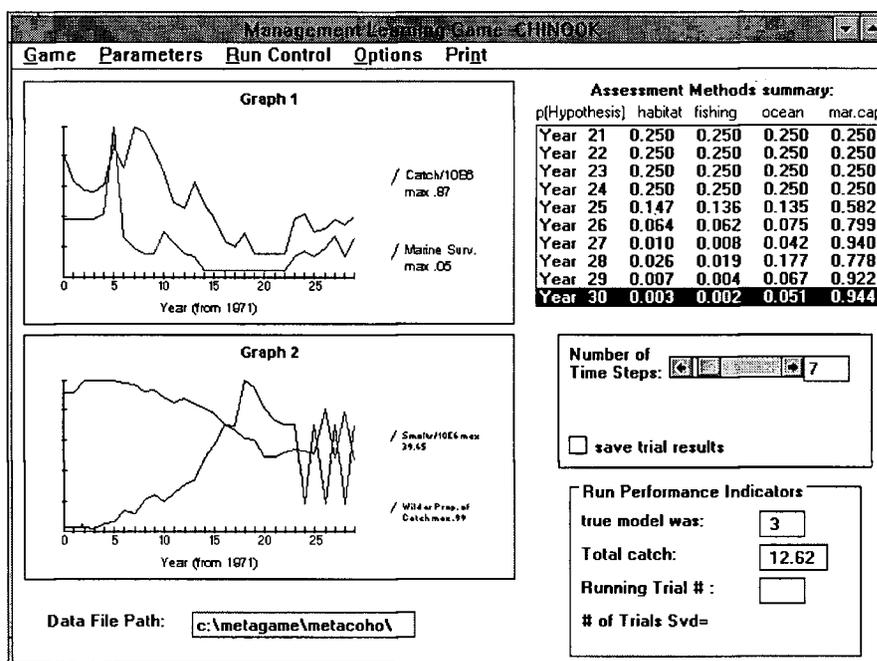
The result of using this equation is that the number of adult fish increases with the total number of smolts provided to the system. This increase reaches an asymptote defined by the adult carrying capacity. At the same time, as the number of smolts increases, the MSR decreases, as would be expected if a carrying capacity limit was in effect.

### 3.2.3. Using the Metagame

This section describes the Metagame interface, the various features of the game, and how the features are used. The game is presented as a series of *forms*, in which the user can either make changes to the parameters that control the game, or observe simulation results. The following description of the program is presented as a guided tour through these forms, and an explanation of what the game player can do in each one.

#### The Management Learning Game (Main) Form

Figure 12. The Metagame main user interface.



The **Main** form (Figure 12) consists of four principle components; the Graph display area, the Assessment Methods Summary, the Run Performance Indicators, and the Control Group.

Most of the **Main** form is taken up by the graph display area. When Metagame is first started, two graphs are displayed there. However, this area can contain up to four graphs, as determined on the **Graph Control** form.

In the upper right hand corner of the **Main** form is the "assessment methods summary" list box. On each line in this box, five items are displayed. First is the simulation year, then comes the likelihood of each of the four hypotheses being true. The likelihoods are calculated based on the data produced by the simulation. For the historical data, where no experiment took place, these likelihoods are set at equal chances for each hypothesis.

Directly below the assessment methods summary is the "control group". This is a set of three controls, each used for a different aspect of the program. The first is the "number of time steps" scroll bar and text box. This scroll bar allows the user to set the number of years over which an experiment is run. The number displayed in the text box is the number of years beyond the end of the historical data that the experiment will run.

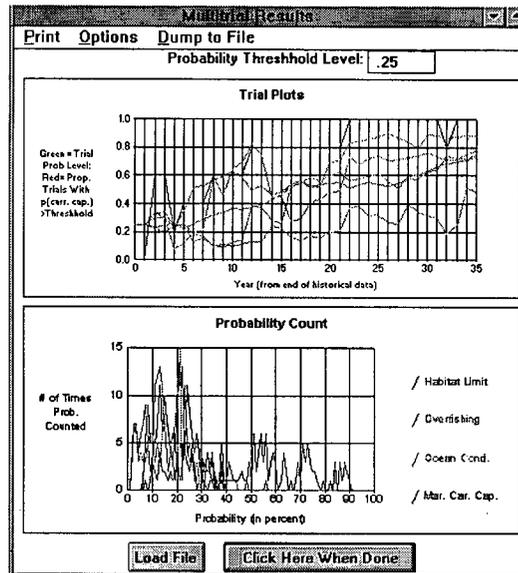
In this same group is the "show multitrial plot" check box. Clicking on this box loads the **Multitrial Plots** form which is used to evaluate the outcome of a multiple run. The final control in this group is the "save trial results" check box. Clicking on this box tells the program whether or not the user will be saving the results of a multitrial. (The program saves multitrial results automatically, unless this check box is clicked off.)

In the bottom right hand corner of the main form is the "run performance indicators" box. In this box are four display areas, which provide the user with different information about the current simulation. The most important is the "true model was" text box which tells the user which hypothesis was chosen by the program to be true.

### **The Multitrial Plots Form**

The two graphs on the **Multitrial Plots** form (Figure 13) are useful in evaluating the results of a multiple run. The first graph is labelled "Trial Plots". The x-axis shows the number of years over which the multiple runs have been carried out, and does not include the historical data years. In other words, the x-axis shows the length of the experiments.

Figure 13. The multitrial plots form shows the patterns in probabilities placed on the various hypotheses.



On this graph, one set of lines are derived from the likelihoods of hypothesis 4 being true at each year. For example, one line plots the likelihood of hypothesis 4 being true from the end of the 23 years of historical data to the end of the experiment, for the first trial. The next line plots the probabilities for the next trial and so on, until there are as many lines as there were simulations, or trials, run.

It should be noted that the words simulation, run and trial are used interchangeably in this context. On the main form, when a multiple *run* is done, the user is prompted for the number of *simulations* to do. This is the same thing as asking for the number of trials to do. (One simulation, run or trial is not the same as one year, but is the same as one *set* of years).

Also shown on this form is a plot over time of the proportion of the trials (i.e. the proportion of the probability lines) that is above a given probability threshold level. This level can be set in the text box at the top of the form. For example, a user might run 100 trials of a 10 year experiment in which the computer chooses hypothesis 4 as the true one. If the probability threshold level is set at 0.25, then at year 9 the proportion line might be at 0.85 on the y-axis. This means that, by year nine of the experiment, 85 out of 100 of the trials showed the Bayes posterior probability of hypothesis 4 being true exceeding 25%. Another way to think about this is as

follows. If 100 separate hatchery managers on different worlds carried out the identical experiment at the same time (i.e., using identical hatcheries in identical environments), then, after nine years 85 of them would calculate, from the data they had gathered, that the probability of hypothesis 4 being true was greater than 25%. By chance, for 15 of them the data would show that the probability of hypothesis 4 being true was less than 25%. Although this graph can take a minute or two to understand, it is the main output of the program, and is extremely useful in understanding how long it might take, under a given experimental regimen, to achieve a result that can be used with confidence, i.e. a probability that is reliably high or low.

The second graph on this page provides another tool for understanding the results of a multiple run. It is a plot of how many times each given probability level occurred for each hypothesis during a multiple run. It counts throughout the whole multiple run, not just for one trial. So, if 100 trials (i.e., experiments) of 10 years each are carried out, and a likelihood is generated for each hypothesis at each year, then each hypothesis will have had 1000 likelihoods generated for it. The "Probability Count" graph simply shows at what level each of those likelihoods fell. So, if a very long set of experiments is carried out, in which hypothesis 4 is set to be true, then the user is likely to see more high likelihoods for hypothesis 4 than any other hypothesis. This graph allows the user to see if that was indeed the case, and in doing so, to check on the power of the assessment method being used.

### **The Graph Control Form**

Across the top of the **Graph Control Form** (Figure 14) is a set of option buttons that allow the user to choose one of the four graph panes. Directly below these option buttons are 14 check boxes, each one providing a data series that can be displayed on a graph. The series among which the user can choose are as follows:

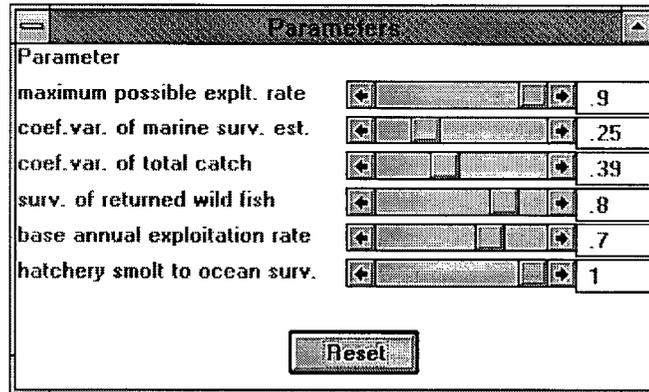
1. **Catch:** Graphs the catch of both hatchery and wild fish in the Georgia Strait. This data series is affected to some degree by random variation.
2. **Marine Survival:** The survival rate of the fish in the marine environment.
3. **Smolts:** The number of smolts released by the hatcheries. When an experiment is carried out, this line is reduced every second year by the amount of the stocking reduction level.

Figure 14. The graph control form allows the metagame user to plot up to four graphs, each showing different information.

4. Wild as Proportion of Catch: The proportion of the catch that is made up of wild, and not hatchery, fish. The general trend in this line is a reduction throughout the historical data for both chinook and coho.
5. P(carr. cap. hyp.): The calculated probability that the carrying capacity hypothesis is true. When a multiple run is done, this line is plotted for each trial on the Trial Plots graph on the **Multitrial Plots** form.
6. Wild Escapement: The number of wild fish that return to spawn.
7. Survival, Model 1-4: Marine survival as predicted by the different hypotheses, 1-4. This is calculated as a function of the marine survival change as set in the **Model Parameters** form.
8. Smolts/Cap, Model 1-4: The number of smolts relative to the capacity set in the **Model Parameters** form. This is calculated as a function of capacity change also set in the **Model Parameters** form.

## The Game Parameters Form

Figure 15. The Game Parameters Form shows the various parameters and default values that affect the running of a metagame.



Parameter	Value
maximum possible explt. rate	9
coef.var. of marine surv. est.	.25
coef.var. of total catch	.39
surv. of returned wild fish	.8
base annual exploitation rate	.7
hatchery smolt to ocean surv.	1

Reset

Six parameters affect the running of a game (Figure 15), and can alter the results of a simulation quite drastically. The default values that appear when the program first starts are best estimates based on currently available data. A description of the parameters follows:

1. Maximum possible exploitation rate: Because the exploitation rate is subjected to some random variation in the model, this simply sets an upper limit on that variation.
2. Coefficient of variation of marine survival estimates: This allows the user to change the amount of variation observed in the marine survival estimates. In essence, this is akin to changing the level of stochasticity in the marine environment, or in our ability to estimate marine survival rates.
3. Coefficient of variation of total catch: This allows the user to change the amount of variation observed in the annual catch. This is akin to changing the level of variation in the ability of fishermen to catch fish, due to some stochastic process.
4. Survival of returned fish: This parameter affects the survival rate of wild fish that are released by fishermen. This only occurs if, during a run that is finished by rules, or a multiple run, the wild catch retention is set to some level other than 1.

5. Base annual exploitation rate: This is the base rate at which the fish are harvested every year. There is some random variation around this level.
6. Hatchery smolt to ocean survival: This is the survival rate of the hatchery smolts before they proceed out to the ocean.

### The Model Parameters Form

Figure 16. The Model Parameters Form shows how the Metagame defines population production under the four different hypotheses.

HYPOTHESIS:	Habitat	fishing	mar-change	mar-cap.
age at recruitment (3=coho, 4=chinook):	4			
Maximum marine survival rate	.008	.008	.02	.02
Marine carrying capacity (mil)	10.	10.	10.	1.5
Fry per spawner (fecundity/2)	2250	2250	2250	2250
Maximum fry-smolt survival	.2	.15	.2	.2
Wild smolt capacity (millions)	100	150	100	100
Annual fry cap change (hab hyp)	.96	1.	1.	1.
Annual marine surv change	1.	1.	.96	1.

Buttons: Read parameters from .MPD file, Save parameters in .MPD file, Done

The **Model Parameters** form (Figure 16) allows the user to alter the parameters that the program uses to simulate the population under each of the four hypotheses. The default parameters are set at best estimates given currently available data. The levels of these parameters define the four hypotheses. For example, under the habitat reduction hypothesis, the annual change in the fry carrying capacity (i.e. available stream habitat) is reduced by four percent every year, while it stays constant under the other hypotheses. In the same way, under the marine carrying capacity hypothesis, the marine carrying capacity is much lower than it is under the other hypotheses, where it is relatively unlimited. The following provides a description of all the parameters:

1. Age at recruitment: This is set at three for coho and four for chinook.

2. **Maximum Marine Survival Rate:** The survival rate of fish during their residence in the marine environment.
3. **Marine Carrying Capacity:** The maximum number of fish that can exist in the marine environment.
4. **Fry Per Spawner (fecundity/2):** Number of fry produced on a per fish basis, regardless of the fish's sex.
5. **Maximum fry to smolt survival:** The maximum survival fish can experience at the earliest life history stages, despite stochastic effects.
6. **Wild smolt capacity:** The maximum number of wild smolts that can survive in freshwater habitats.
7. **Annual fry capacity change:** The reduction in survival of fry to smolts every year. This parameter is important in defining the habitat reduction hypothesis.
8. **Annual marine survival change:** The reduction in the marine survival rate every year. This parameter is important in defining the oceanographic conditions hypothesis.

#### **3.2.4. The Questions that Were Addressed**

In working with the Metagame program, the original question I set out to answer was a simple one. "How long would hatchery managers need to carry out a stocking rate manipulation in order to identify whether or not hatchery released fish are negatively impacting wild stocks in the Georgia Strait? I soon found that the question needed to be stated more explicitly. Specifically, the degree of the manipulation that the managers were willing to make needed to be declared. In other words, would the managers be willing to alternate stocking levels by 90% or only 20%? Also, what degree of certainty was necessary before it would be deemed cause for a permanent change in the hatchery release program? If there was a 10% chance that hatchery releases were reducing wild stocks, would this be enough to convince managers that the release program should be reduced? Or would there have to be a 90% certainty before any permanent action was taken?

After struggling with these difficulties for some time, I realized that the real problem was not in the question, but in my approach to answering it. In order to fully utilize the abilities of the Metagame program, the

answer that should be sought is not simply "You will need to do an experiment for x number of years." There is a definable tradeoff in the number of years an experiment must be run, versus the degree of the manipulation that is made, and versus the degree of certainty that is required. Therefore, I turned my efforts to defining this tradeoff under different parameter settings and the different hypotheses. The following results section describes that tradeoff and helps to answer the original question for different degrees of certainty and stocking reduction rates. It also helps to define a more specific question to be tested by the model in the future.

### **3.2.5. Simulations Run**

In testing the Metagame, I ran over 70 simulation experiments, each one varying a single parameter. Each experiment was run for 55 years, and for 100 trials. In other words, each of my single experiments was analogous to 100 different hatchery managers running the same 55 year experiment under identical conditions. The length of the experiment was intentionally chosen to be very long. This was done to allow me to report on the conditions of the population at any time during the experiment. In other words, I was able to see what would have happened had the experiment been run for any time shorter than 55 years, as well as for the entire 55 years. By running 100 trials of each experiment, I was able to identify the degree of variation caused by stochastic effects.

The results reported here are based on manipulations of four of the Metagame's parameters. While it is certainly possible to vary more than these four, it was not deemed useful to spend too much time altering other parameters for two reasons. First, the different possible combinations of parameters rapidly approaches a staggering number (in the hundreds of trillions) if they are all taken into account. Second, and more importantly, three of the four parameters I varied are the only ones that fisheries managers have the ability to alter. These three parameters were:

1. The degree to which hatchery releases were reduced every second year.
2. The percentage of the wild catch that was retained by fishermen.
3. The exploitation rate of the entire stock, both hatchery and wild.

The fourth parameter that I varied was the hypothesis that defined the true situation in the Georgia Strait. Admittedly, this parameter is not within a manager's abilities to alter. However, since we don't know which hypothesis is actually true, it was important to test the results of manipulations under all of them. Table 11 shows a listing of the experiments on which I based the results presented below. All the manipulations listed in Table 11 were done for both coho and chinook.

*Table 11. The parameter settings which defined the manipulations tested. All manipulations were carried out for both chinook and coho over 55 year runs and 100 trials.*

True Hypothesis	Stocking Reduction Levels	Wild Catch Retention	Exploitation Rate
4	0.25, 0.35, 0.45, 0.55, 0.65, 0.75, 0.85, 0.95, 1.0	1	Default (Chinook = 0.7 Coho = 0.8)
4	0.25, 0.65, 0.85, 0.95	0	Default
4	0.25, 0.65, 0.95	1	0.95
4	0.25, 0.65, 0.95	1	0.25
3	0.55, 0.75, 0.95	1	Default
3	0.55	1	0.25
2	0.55, 0.95	1	Default
2	0.55	1	0.25
1	0.55, 0.95	1	Default
1	0.55	1	0.25

### 3.3. RESULTS AND DISCUSSION

#### 3.3.1. Manipulation of Stocking Reduction Levels, Hypothesis 4 (Marine Carrying Capacity) True

The first question I set out to answer was, "How does the amount of time it takes to detect whether or not hypothesis 4 is true vary with the degree to which hatchery releases are reduced?" In order to explore this question, I ran simulations at nine different stocking reductions. I set hypothesis 4 to be true for all of them. The stocking reduction ranged from 25% up to 100%. It is important to note that the Metagame program simulates stocking reductions as occurring every second year. This produces paired contrasts between the years when the reduction occurs and the years when stocking levels are normal.

Running simulations at different stocking reductions produced a clear pattern. At high stocking reductions, a greater proportion of the trials showed high probabilities of hypothesis 4 being true at earlier years. In essence, this means that if hatchery releases are reduced by a large amount, an experiment is more likely to correctly identify that hypothesis 4 is true in a short period of time. This is to be expected, since the more hatchery releases are reduced, the greater is the contrast provided for the experiment to detect. Figure 17 shows this relationship for chinook and coho.

Some interesting results of varying the stocking reduction can be seen in Figure 17. While the stocking reduction level was increased by a uniform amount for every trial (10%), the ability to detect that hypothesis 4 was true did not increase uniformly. Much greater increases are seen among lower stocking reduction levels than higher ones. This is particularly evident in the case of the coho population, but the pattern holds true for chinook. For example, in the coho graph, it can be seen that an increase in the stocking reduction level from 25% to 45% shows a much greater impact than an equivalent increase from 75% to 95%. This suggests that, if the goal of the experiment is to learn whether or not hypothesis 4 is true as quickly as possible, much greater gains can be made by increasing stocking reductions when they are at low levels than when they are already at high levels. Therefore, if a decision is being made whether to increase the amount of stocking reduction from 25 to 35%, it should be considered much more seriously than a decision to change stocking reductions from 85 to 95%.

The same sort of diminishing return can be seen in the amount of time over which an experiment is run. Particularly at higher stocking reduction levels, the greatest amount of learning goes on in the earliest years of an experiment. The change in how sure we can be that hypothesis 4 is true is much greater between years 0 to 10 of an experiment than it is between years 45 and 55. Once again, this suggests that more weight should be given to the decision to lengthen a short experiment than to lengthen an already long experiment.

One other policy decision is implied by this pattern of diminishing returns. At some point, it will no longer be profitable to increase the stocking reduction level, or to increase the number of years over which an experiment is run. The amount of information that can be gained by increasing the manipulation will not be worth the investment that must be made to provide such an increase. Therefore, there should be an upper bound on the amount by which hatchery releases are reduced, and the number of years for which an experiment is run. This upper bound will be

set, at least partly, by economic factors. How much does it cost to increase the harshness of the manipulation, and how much does a year's worth of experimentation cost? How much will be gained from the resulting information?

Figure 17. The proportion of trials that showed the probability of hypothesis 4 being true to be greater than 90% when hypothesis 4 was in fact true. Trials were run at 9 different stocking reduction levels, from 25% through 100%.

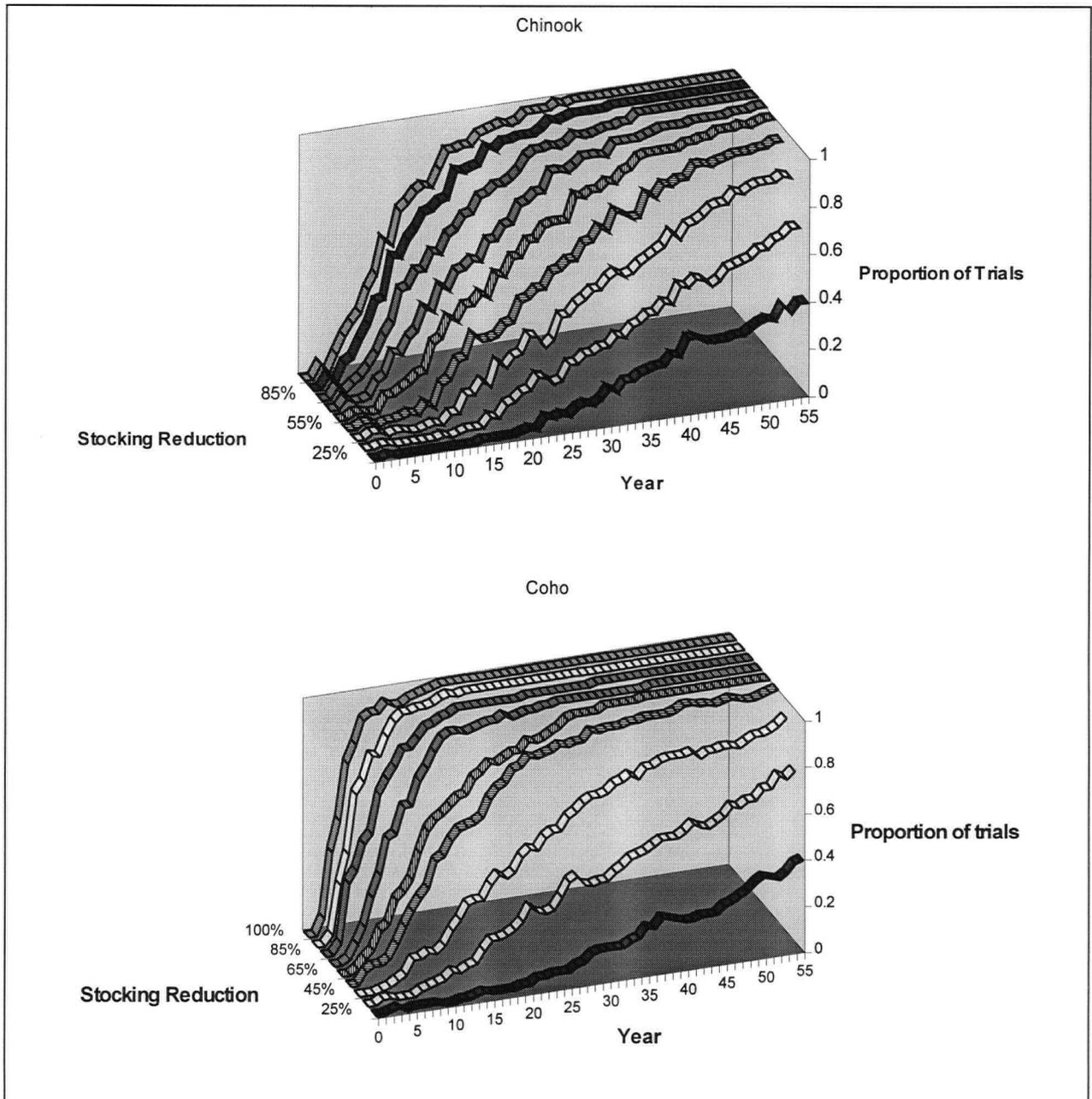


Figure 17 gives a qualitative idea of the changes that occur over a continuum of different stocking reduction levels. However, it is difficult to see from this figure how to reach quantitative conclusions about the number of years it takes to reach a desired level of certainty. This is more easily derived from Figure 18, which contains some of the same information as Figure 17, but is presented in a more quantitative manner.

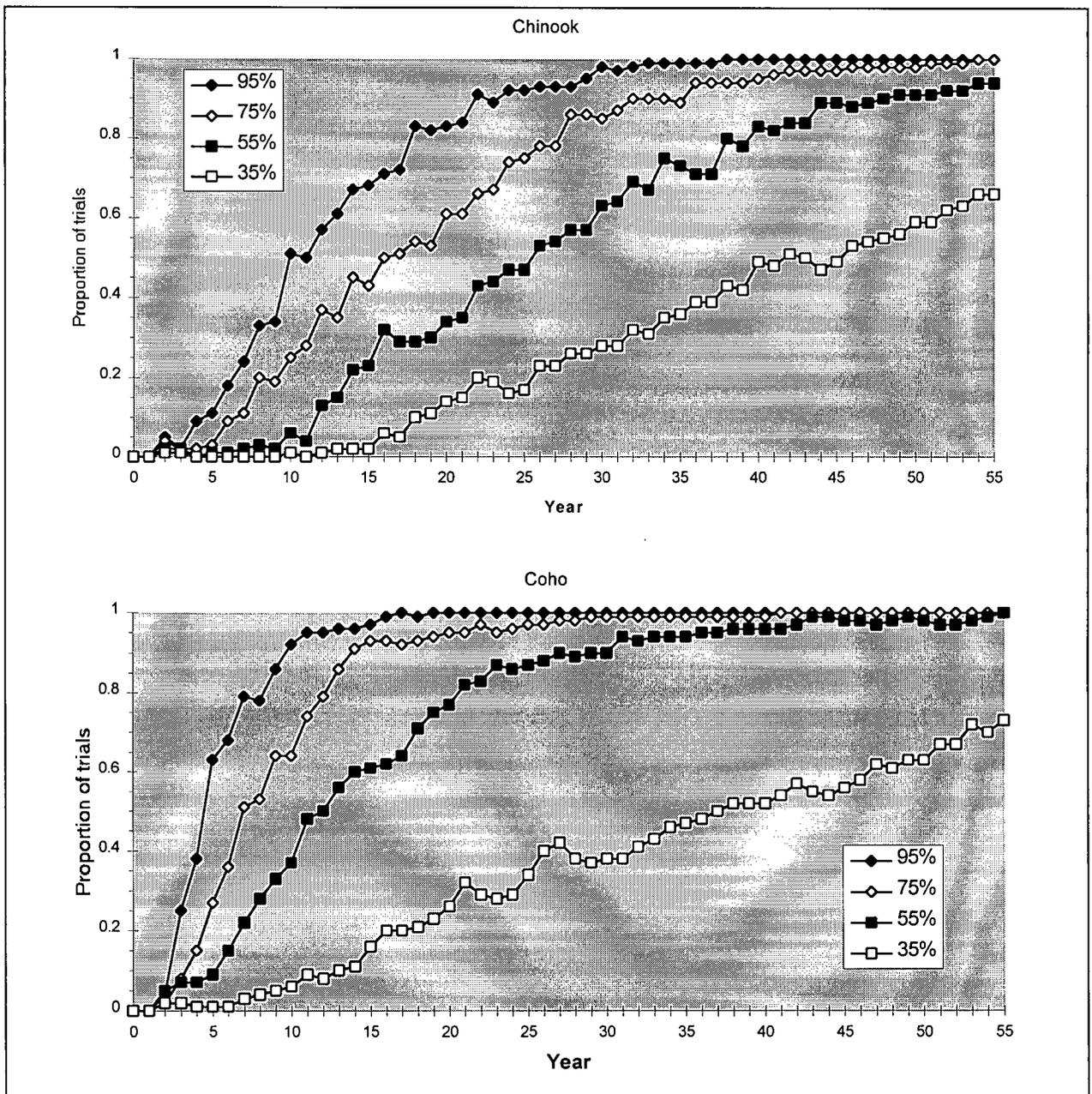
Using Figure 18, one can start to answer the question "How long will it take to learn whether or not hypothesis 4 is true?" Of course, to begin with, it is still necessary to arrive at a decision as to what level of stocking reduction is reasonable to undertake. However, in light of the information provided in Figure 17, it is apparent that, if an economic limitation exists, it is probably best not to invest in a stocking reduction that is too high. By the same token, an extremely low stocking reduction is also undesirable, as just a small increase in stocking reductions at low levels can significantly reduce the time to learn. Therefore a stocking reduction level that is high, but not too high, is best. Consider a 75% reduction of chinook stocking as an example.

It is necessary to start by defining what proportion of the trials one is concerned with. For illustrative purposes, this might refer to the number of trials, out of 100, that show a probability of hypothesis 4 being true to be greater than 90%. Another way to look at the proportion of trials is to think of it as the probability of any single experiment working. That is, if a manager was to run only one experiment, instead of 100 (which seems likely) what is the probability that it would show hypothesis 4 to have a likelihood of greater than 90% at any given year, if in fact, hypothesis 4 was true. As an example, I will arbitrarily define 95% as the proportion of trials I am interested in. This gives an experiment an almost certain chance of working.

Thus, an appropriately specific question has been defined, given the information at hand. "How many years will it take for an experiment to show hypothesis 4 to be at least 90% likely to be true, if we reduce stocking rates by 75% every second year? I want to have a 95% chance of this experiment working." These levels of certainty are fairly high, and this example could probably be considered as one in which the manager wants to be as sure as possible that hypothesis 4 is true before he takes any action to permanently alter his hatchery releases. Of course, the hatchery manager will have to run his experiment for a very long time in order to gain this level of certainty. From the chinook graph in Figure 18, it can be seen that the 75% stocking reduction line reaches a level of 95% of the trials at about 46 years. This is probably an unreasonably long experiment. However, before

discussing ways in which a shorter experiment might suffice, I will examine the results for the coho population, as shown in Figure 18.

Figure 18. The proportion of trials that showed the probability of hypothesis 4 being true to be greater than 90% when hypothesis 4 was true. Trials are shown for 4 different stocking reduction levels, from 35% through 95%.

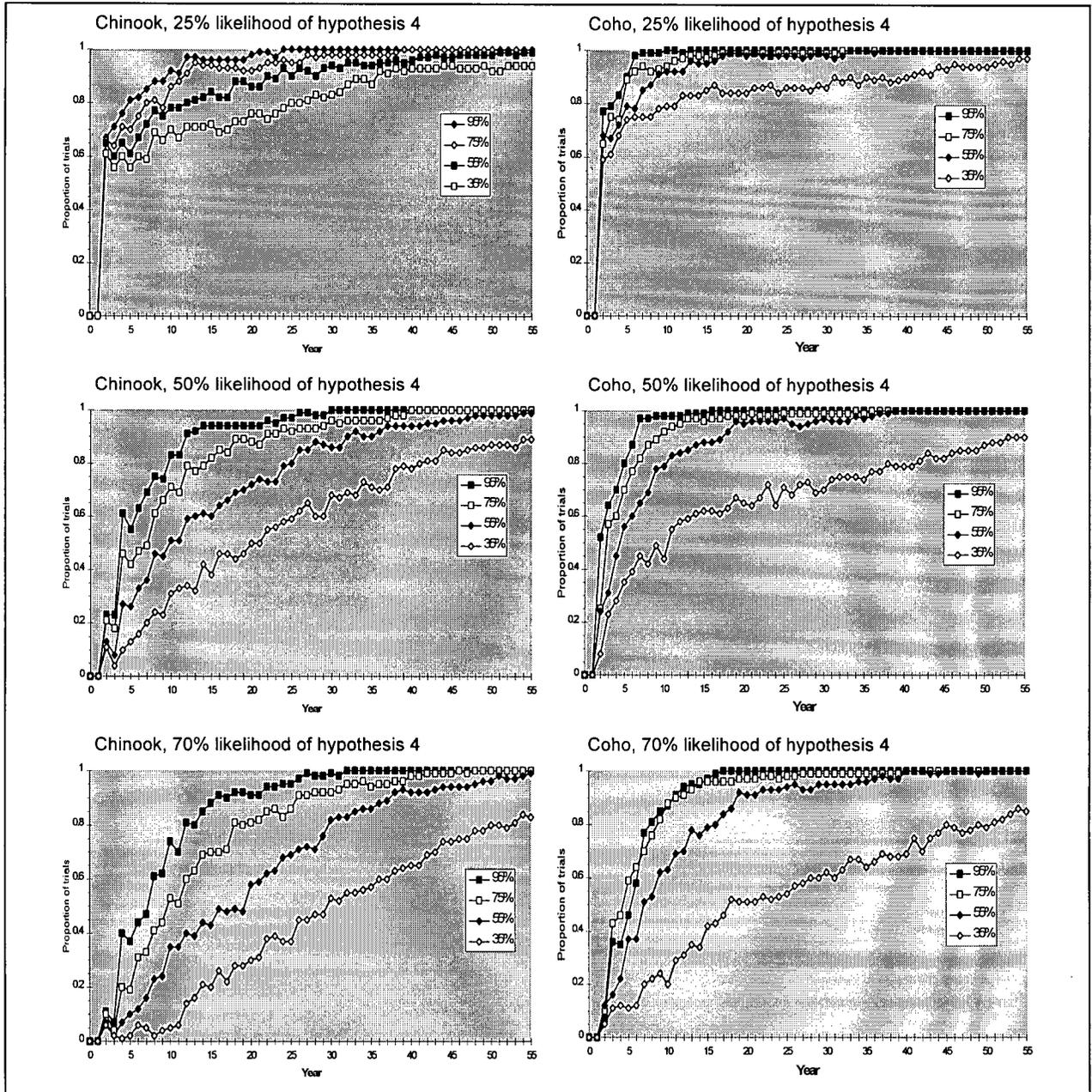


Using the same requirements we set above, one can see how long it would take to learn that hypothesis 4 was true if the experiment was run with the coho population. Looking at the coho graph in Figure 18, for the 75% stock reduction line, 95% of trials show a likelihood of 90% or greater after about 20 years. While this is considerably better than the equivalent case with the chinook population, it is quite possible that 20 years is still too long an experiment to justify even starting it.

The easiest way to reduce the number of years required to show that hypothesis 4 is true is to lower the level of certainty required. For example, if it is decided that a likelihood of 30% that hypothesis 4 is true is enough to dictate a permanent change in the levels of hatchery releases, the length of the experiment can be much shorter. For chinook, at a stocking reduction level of 75%, 95 out of 100 experiments will show a likelihood of 30% or better for hypothesis 4 after only 11 years. This is a substantial improvement over 46 years, as discussed in the previous example. For the coho population, with the same level of stocking reduction, it only takes about 7 years for 95% of the trials to show a likelihood of 30% or better that hypothesis 4 is true.

It is not easy to decide on the appropriate level of certainty to use. This level depends on many factors, chief among them being the relative weight given to the importance of the hatchery release program versus the wild salmon stocks. This is an issue that must be decided by those who wish to halt the decline of the wild stocks, and those who stand to benefit from keeping hatchery releases at their current levels. The only general statement that can be drawn from simulations using the Metagame program is that greater levels of certainty demand longer experiments and higher stocking reduction levels. Figure 19 shows the results of simulations for several different levels of certainty. Using these graphs, one can pinpoint how many years an experiment might take given a specific level of certainty and a specific stock reduction.

Figure 19. The proportion of trials that showed a specific likelihood of hypothesis 4 being true. Trials were run for 4 different stocking levels, from 35% through 95%. Graphs are shown for both coho and chinook populations.



### 3.3.2. Manipulation of Wild Catch Retention, Hypothesis 4 True

Once I had experimented with the stocking reduction levels, I wanted to see if there were other policy changes fisheries managers could make that would reduce the time to learn. One such change the model allows is in

the proportion of wild catch that is kept by fishermen. This policy alternative is primarily intended as a method to rebuild wild stocks while the experiment is going on, but I wanted to see how it would affect the amount of time it took to decide whether or not hypothesis 4 was true.

The result for both chinook and coho was quite clear. Any reduction in the proportion of wild catch retained did, in fact, lead to a rebuilding of the wild stock during the experiment. The degree of rebuilding depended on the proportion of wild stocks that were thrown back, as would be expected. However, rebuilding the wild stocks in this manner also increased the amount of time it took to learn whether or not hypothesis 4 was true. This was particularly true in the case of chinook manipulations, which always took a longer time to produce any level of certainty about the true hypothesis than the coho did. This result is not surprising when one considers the overall effect of rebuilding the wild stocks during an experiment. This causes the hatchery stock to become a less significant percentage of the total stock in the Strait, so that any manipulation in the levels of hatchery stock becomes a smaller manipulation in terms of the total stock. A smaller manipulation provides less contrast, and therefore the experiment takes a longer time to produce a result.

Figure 20 shows the 0% wild catch retention line in a 95% stocking reduction experiment. This can be compared to the 95% stock reduction line with 100% wild catch retention, shown on the same graph (as the default line). A 0% wild catch retention means that all wild fish that are caught are thrown back. This is the most extreme case possible. It is shown on the graph to clearly illustrate that a reduction in wild catch retention leads to increased learning time. The same is true for smaller reductions in wild catch retention, but the learning time is not increased to the same degree.

From the graphs, it can be seen that, for chinook, a 100% retention of wild catch leads to 95% of trials showing hypothesis 4 to be greater than 90% likely in about 28 years. However, with a 0% wild catch retention we never reach this level over the entire 55 year experiment. The case with the coho, as always, is not quite as extreme. Under a 100% catch retention, it takes about 11 years to show that hypothesis 4 is true. With 0% wild catch retention, this time is increased to about 20 years.

The implication of these results is clear. Any attempt to rebuild wild stock during an experiment designed to learn whether or not hypothesis 4 is true is likely to increase the amount of time it takes to reach an acceptable

result. Smaller reductions in the wild catch retention rate will not impact the time to learn as dramatically, but any change will lengthen the experiment to some extent.

### **3.3.3. Reducing Exploitation Rates, Hypothesis 4 True**

The final manipulation I explored in my attempt to reduce learning time was the base exploitation rate parameter. Increasing or decreasing this parameter changes the degree to which fishing impacts the total stock in the Georgia Strait, both wild and hatchery.

When exploitation rates are reduced, the situation is much the same as reducing the retention of wild fish in the catch. A larger standing stock of both hatchery and wild fish is left in the Strait every year. This has the effect of reducing the degree of contrast that can be obtained by a controlled fluctuation in hatchery releases. As would be expected, this increases the time it takes to learn that hypothesis 4 is true. Looking again at Figure 20, the "learning curve" under a 25% exploitation rate can be compared with the default curve.

Once again, for the chinook, a reduction in the exploitation rate leads to a situation in which even after 55 years of experiment, a very low proportion of trials has reached a 90% likelihood that hypothesis 4 is true. For the coho population, a 25% exploitation rate produces a curve very similar to that produced by a 0% wild catch retention. Once again, the time to learn that hypothesis 4 is true is increased from 11 to about 20 years.

The implication of this result is very clear. Increasing the standing stock in the Strait by reducing exploitation rates increases the time for a hatchery release experiment to produce an acceptable result. While it may be desirable to reduce exploitation rates in order to increase standing stock size, the negative impact it would have on a hatchery release experiment should be considered.

### **3.3.4. Increasing Exploitation Rates, Hypothesis 4 True**

The obvious extension to the previous manipulation is to find out what happens when exploitation rates are increased. The result of this manipulation is not as straightforward as that of reducing exploitation rates.

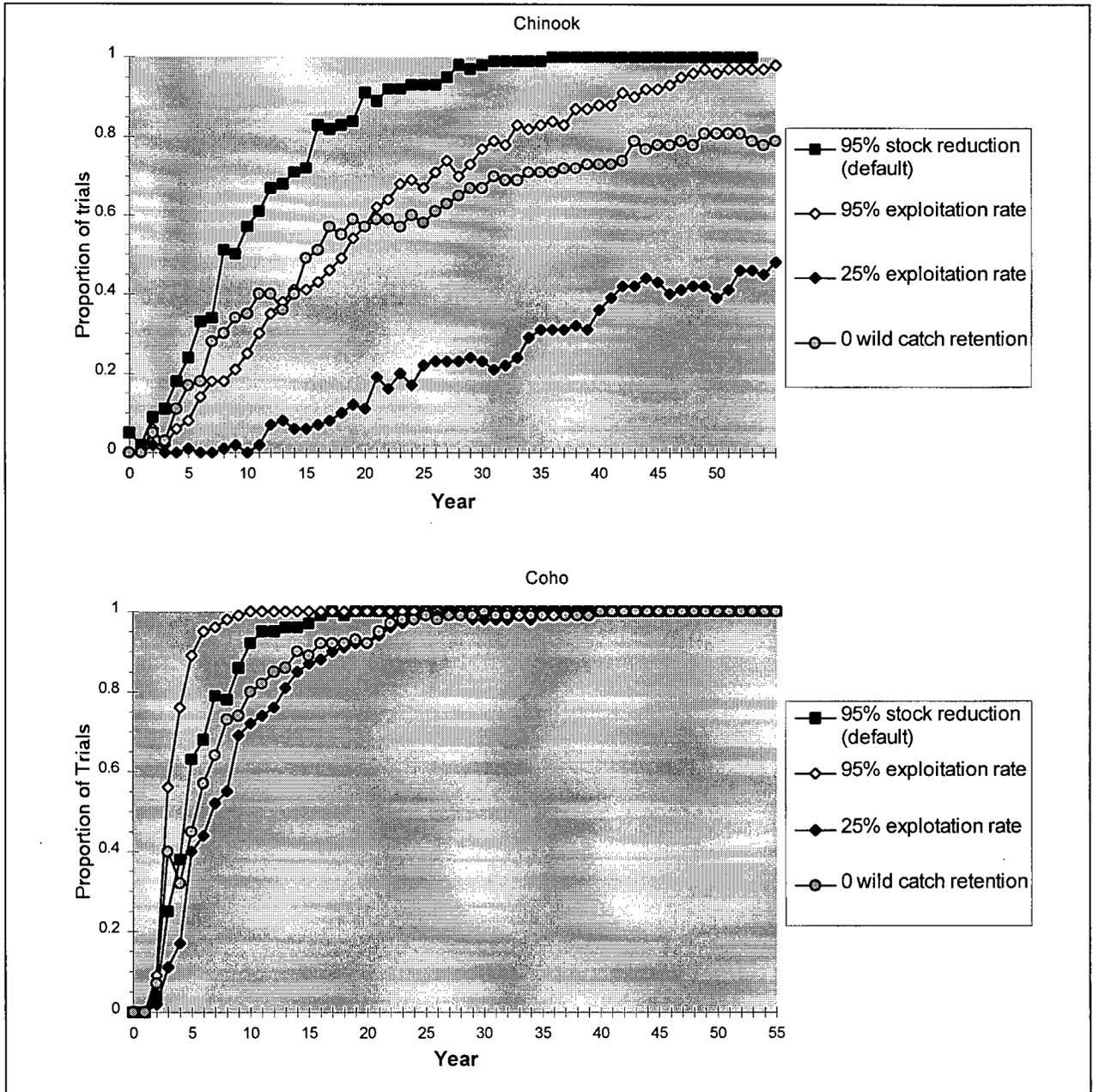
In the case of the chinook population, the default exploitation rate is set at 70%. This was compared with an increased exploitation rate of 95%. Initially, I expected that by increasing the exploitation rate to this extreme

level, I would cause the program to simulate a decrease in the standing stock. Then, any fluctuation of hatchery releases would produce a relatively high level of contrast, and the time to learn that hypothesis 4 was true would be decreased. However, this did not occur. For the chinook, when exploitation rates reach 95%, the wild stock is driven almost to extinction, and the standing stock is, indeed, reduced. However, the impact on stocks is so great that the program has a difficult time distinguishing this situation from one in which overfishing is the cause of the wild stock decline. In fact, by simulating such an extreme exploitation rate, we have produced a situation in which both overfishing *and* a marine carrying capacity are negatively impacting the wild stock in the Strait. This means that it takes the program longer to determine that hypothesis 4 is true, and learning time is hence increased.

From the first graph in Figure 20, it can be seen that an increase in exploitation rate from the default level (70%) to 95% increases the time to learn that hypothesis 4 is true from 28 years to about 49 years. This result has interesting implications for a chinook hatchery experiment. There is apparently an ideal level of chinook exploitation (neither too high nor too low) that will produce an experiment that will allow us to determine the situation in the Strait in the shortest amount of time. While I have not run enough simulations to determine the exact level, we can be reasonably sure that it is not higher than current exploitation rates, since a relatively small increase produced an increase in learning time. This implies that, in the case of the chinook stocks, the best policy would probably be to not allow exploitation rates to increase from their current levels. At the same time, if a short experiment is of paramount importance, it might be preferable to reduce exploitation rate to some small degree, but the results argue against any large reduction. While further simulations would have to be done to determine the ideal exploitation rate in terms of a short hatchery experiment, it appears that current exploitation rates seem to be reasonably good at producing short learning times.

Increasing exploitation of the coho population produces a different result. From the coho graph in Figure 20, it can be seen that an increase in exploitation (from 80% to 95%) *reduces* the amount of time it takes to learn that hypothesis 4 is true. Under default exploitation rates, it takes about 11 years for 95% of the trials to agree, while a 95% exploitation rate reduces the time to only about 6 years.

Figure 20. The proportion of trials that showed the probability of hypothesis 4 being true to be greater than 90% when hypothesis 4 was true. Trials were done at different exploitation rates and wild catch retentions.



This result suggests that my original expectations are true for the coho population. It also indicates that the simulated chinook population is much closer to being over-fished than the coho population. In fact, even at a 95% exploitation rate the coho population did not appear to be recruitment over-fished. However, increased exploitation

rates did have a negative impact on wild stocks, particularly in the hatchery release years. This threat of extinction for the wild stocks argues against allowing exploitation rates to increase, even if it would decrease the amount of time for which a hatchery experiment would need to be run. At the same time, coho exploitation should probably not be decreased, as this would necessitate a longer hatchery experiment in order to illuminate what the true situation in the Strait is.

### 3.3.5. The Other Hypotheses

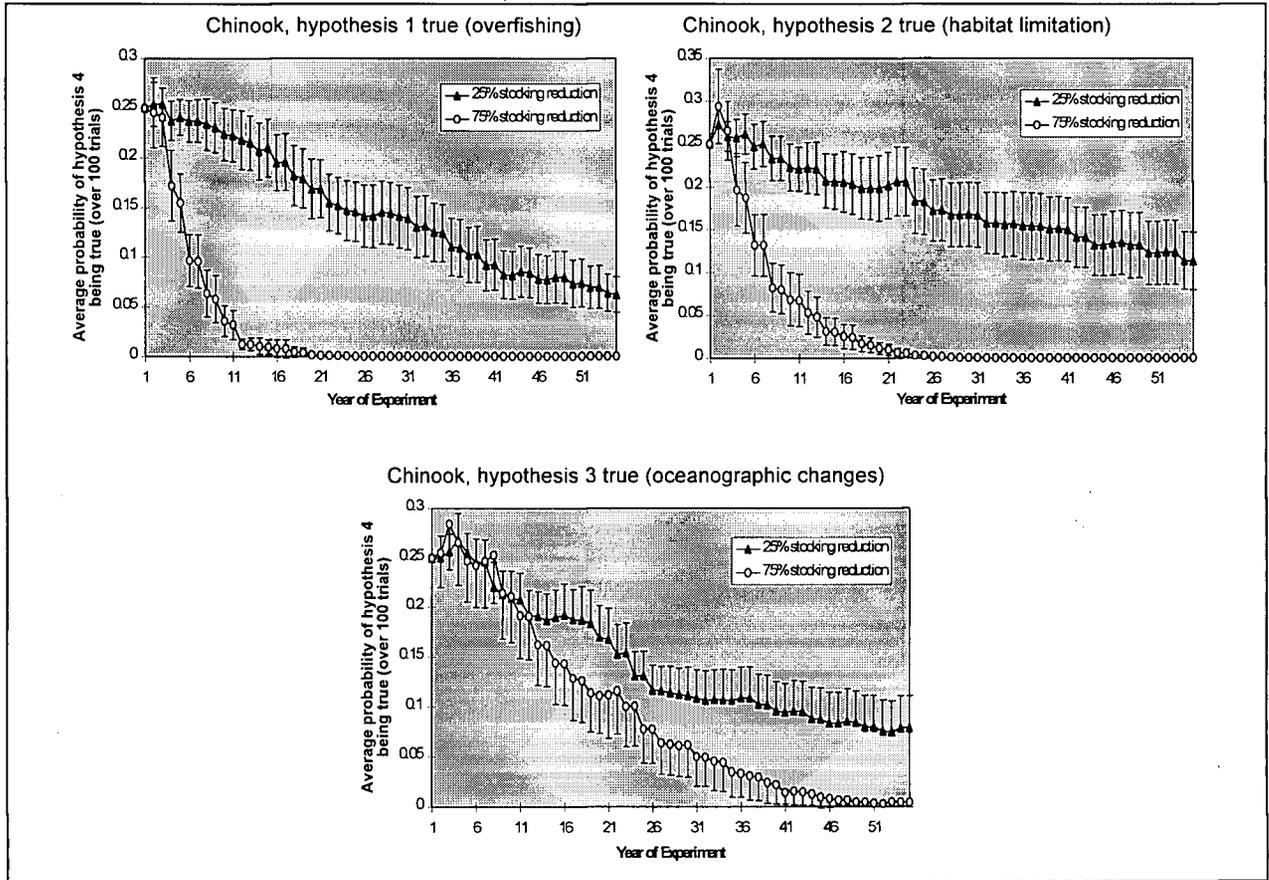
To this point, I have only discussed simulation experiments that were carried out when hypothesis 4 was set to be true. This begs the question, "What happens when the other hypotheses are true?" Obviously we cannot assume *a priori* that hypothesis 4 defines the real situation in the Georgia Strait, or there would be no point in doing a hatchery experiment in the first place. So, if one of the other hypotheses is true, how quickly can we learn that hypothesis 4 is *not* true? Is the learning time shorter in this situation than when hypothesis 4 *is* true? Can we disprove hypothesis 4 faster with some of the alternative hypotheses than others?

To answer these questions, the obvious first step is to run trials using the alternative hypotheses and compare them to trials run using hypothesis 4. When an alternative hypothesis is run, the probability of hypothesis 4 being true starts at 25% (as do all the other hypotheses) and drops off to very low levels, usually to zero. The rate and magnitude of this decline both depend on the degree of manipulation of stocking rates. Eventually, if the experiment is run long enough and has a significant manipulation of hatchery releases, the probability of hypothesis 4 being true drops to 0% for all the trials of a multitrial. The complicating factor is that, sometimes, the probability of hypothesis 4 being true initially *increases*, and does not drop off until after a fairly long experiment has been run. Or, the probability of hypothesis 4 can be low, then increase in the middle of an experiment, and return to low levels. These apparently anomalous results come from the fact that the data the computer generates for comparison to the hypotheses have a random component to them. So, with some experiments, the other hypotheses can produce data that look like hypothesis 4 is true.

Conversely, when a set of trials is run in which hypothesis 4 *is* true, the probabilities start at 25% and increase until they are all, eventually, at 100%. However, while some of the trials increase to 100% probability very

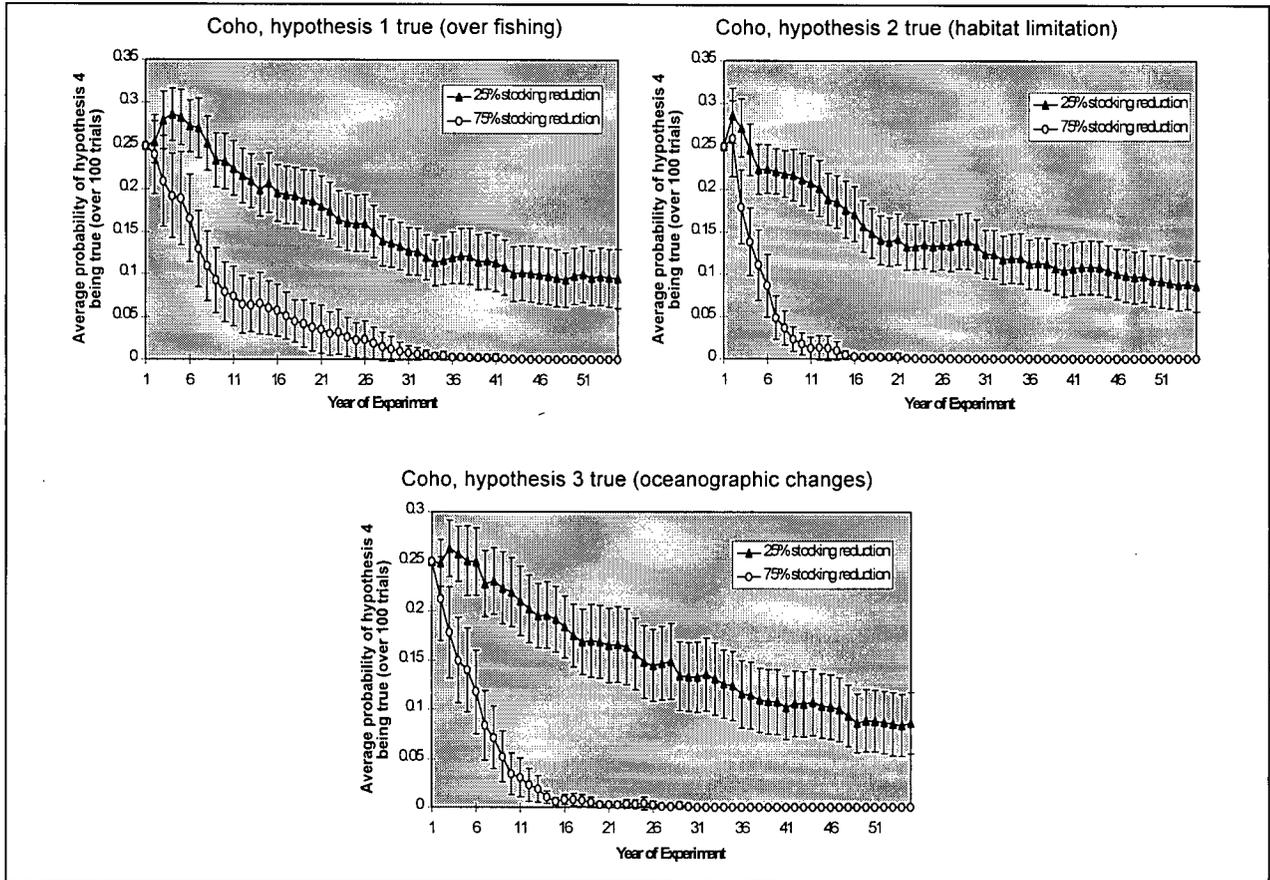
rapidly, others stay at low probabilities for a long time, and only increase after a very long experiment. Still others fluctuate up and down before they finally increase to 100% probability. So, the problem becomes one of distinguishing random effects from the effects seen when hypothesis 4 is true.

Figure 21. Chinook: decline in the estimated probabilities of hypothesis 4 being true when the other hypotheses were true. Error bars show 95% confidence intervals,  $n=100$ . (Note: some error bars omitted for clarity).



Figures 21 and 22 show time plots of the decrease in the estimated probability of hypothesis 4 being true when the other hypotheses are true. These graphs show how efficient the metagame program is, on average, of detecting the fact that hypothesis 4 is not true.

Figure 22. Coho: decline in the estimated probabilities of hypothesis 4 being true when the other hypotheses were true. Error bars show 95% confidence intervals, n=100



For all the hypotheses, it is readily apparent that the intensity of the manipulation influences learning time in exactly the same way as it did for the hypothesis 4 experiments. In other words, the greater the degree of hatchery release fluctuations, the shorter will be the time to learn that hypothesis 4 is not true. In the same way, reducing manipulation intensity will slow learning time, no matter which hypothesis is true. For example, in the case of chinook, where the overfishing hypothesis (hypothesis 1) was set to be true, it took around 20 years for all experiments to assign a 0% probability to hypothesis 4, when a 75% stocking reduction was used. However, when the stocking reduction was decreased to 25%, even after 55 years the average experiment still assigned a reasonable probability (around 10%) to hypothesis 4. These results are intuitive if one returns to the idea of contrast. In making a more extreme manipulation, one expects a more extreme response if hypothesis 4 is true. If this response

does not occur it is more readily apparent than if only a small manipulation was made to begin with. Therefore, a more extreme manipulation allows the experiment to show that hypothesis 4 is not true more quickly than a mild manipulation does. It is interesting to note that, at least for the chinook population, when hypothesis 3 is true, increasing stocking reductions produced the smallest decreases in learning time. In other words, it appears that an increase in stocking reduction levels is least beneficial when hypothesis 3 is true.

The 95% confidence intervals displayed on Figures 21 and 22 illustrate another interesting effect of increased stocking reductions. For the high stocking reduction experiments, the variability in results decreases rapidly, as indicated by the shrinking confidence intervals. However, with stocking reductions of only 25%, there is some degree of variability in experimental results, even after 55 years. This means that, after a few years, a low stocking reduction experiment is more likely to show erroneously high probabilities of hypothesis 4 being true than a high stocking reduction experiment. Again, this effect is due to the decreased level of contrast available to be detected.

Using the Metagame program, if we show that hypothesis 4 is not true, can we say anything about which of the other three hypotheses *is* true? Since the experiment that is simulated by Metagame is only designed to alter the situation in the Georgia Strait if hypothesis 4 is true, it is much easier to make assertions about it than the other hypotheses. However, using the Probability Count graph on the **Multitrial plot** form, it is sometimes possible to draw some conclusions about the other three hypotheses, depending on the degree of the manipulation made. When a trial is run in which one of the first three hypotheses is true, this graph usually counts more high probabilities for this hypothesis than the other three. In this situation, hypothesis 4 usually shows a large number of calculations in which the estimated probability was 0.

From figure 21, it is interesting to note that it is generally easier to distinguish hypothesis 4 from hypotheses 1 and 2 (overfishing and freshwater habitat loss) than it is to distinguish hypothesis 4 from hypothesis 3 (changing oceanographic conditions). This is particularly true in the case of the chinook population. This result implies that if hypothesis 1 or 2 is true, a hatchery reduction experiment will start to produce low probabilities of hypothesis 4 very quickly. If hypothesis 3 is true, it may take longer to verify that hypothesis 4 is *not* true.

### 3.3.6. Conclusions

Exploring different experimental manipulations with the Metagame model, I have been able to draw some general conclusions. Regardless of which hypothesis really *is* true, the following steps outline methods by which a manager can reduce the time it takes to learn whether or not there is a marine carrying capacity in the Georgia Strait:

1. Increase the violence of fluctuations in hatchery releases.
2. Ensure that exploitation rates are not reduced during the experiment. (Exploitation rates should probably not be allowed to deviate from their current levels.)
3. Do not attempt to rebuild wild stocks through some other policy manipulation.

Since the actual number of years an experiment takes depends on the level of certainty required, as well as the degree of hatchery release fluctuations that can be produced, it is not possible to determine exactly how long an experiment would require to discover whether or not there is a carrying capacity limit in the Georgia Strait. However, an example of a "reasonable" experiment can be given. Suppose it were possible to reduce hatchery releases by 75% of their current level every second year, that we would accept the carrying capacity hypothesis as being true if the experiment produces a 70% or higher likelihood, and that we want to be 95% sure that the likelihood will be at least this high if the carrying capacity hypothesis is true. From the modelling simulations I have run, the Metagame suggests that such an experiment would take about 30 years in the case of the chinook population. For coho, the model suggests such an experiment could take as long as 14 years. By reducing hatchery releases more (say, 95% every second year) we can complete a chinook experiment in about 20 years. A coho experiment can be reduced to 12 years.

There is an important point to be made about these estimates of experiment length. To produce them, we are looking for the point where 95 out of 100 theoretical experiments produces the desired result. This is to ensure that no matter what happens in the real experiment, we will achieve the correct result. However, of these 95 theoretical experiments, it does not take the full amount of time for all of them to reach the desired level of probability. In fact, most of them take less time, and some of them are very much faster. In fact, after only 3 or 4

years, a small proportion of them have already reached the desired level of probability. In other words, the number of years predicted above are worst case scenarios. There is quite a good chance that any experiment undertaken by the hatcheries will not take the full amount of time to complete. By the same token, there is a small (5%) chance that the experiment will take even more years to complete. Therefore, in designing an experiment, the maximum amount of time should be allowed for, but it is possible that it would not take this long to achieve the desired likelihood indicating whether or not hypothesis 4 is true.

Finally, it is important to attempt to draw some conclusions regarding practical use of the Metagame model. In order to gain the maximum benefit from the model, it should continue to be used while designing and carrying out a hatchery release manipulation. As different levels of manipulation are considered, the program can be used to evaluate them. Estimates of the time necessary to learn under a given manipulation, and the degree of certainty that can be achieved should prove useful in deciding whether or not a specific manipulation has a favorable cost/benefit ratio. This should be useful to fisheries managers in deciding whether or not it would be worthwhile to even begin a hatchery experiment.

Once such an experiment was started, the program could be used to evaluate the probability of any results obtained, if the carrying capacity hypothesis is true. For example, if an experiment showed a low probability of the carrying capacity hypothesis being true, Metagame could be used to run a large number of trials under the same experimental regime, for the same amount of time. From the results of these trials, it would be possible to estimate the likelihood that the low result was produced spuriously, out of random variability. This process would be useful in avoiding the early termination of an experiment based on results that were random, as opposed to results that accurately reflected the situation in the Georgia Strait. Thus, the model could be a useful tool throughout the entire experimental process, from design to completion.

## CHAPTER 4: GENERAL CONCLUSIONS

Due to long term increases in hatchery releases, with little or no corresponding increase in overall catches of Georgia Strait coho and chinook, concern has arisen regarding their future. The aims of this thesis were to examine the possibility that a carrying capacity limit is responsible for the apparent decline in survivals of juvenile salmon, and to suggest hatchery manipulation experiments to test for the limit.

The results of a direct feeding study suggest that juvenile salmon may have a much greater impact on available food resources than has previously been suspected. Considering the other species in the Strait that utilize the same foods, as well as the turnover rate of the prey species, it appears that the coho and chinook populations may have become large enough that they have reached a carrying capacity limit. This conclusion is reinforced by the low feeding rates that were estimated by a bioenergetics model of salmon growth and feeding.

However, the feeding results must be viewed with caution. Several suspect parameters were used in estimations of smolt diet patterns and food availability. Better estimates of zooplankton abundances and juvenile mortality rates are necessary to provide more conclusive results. Also, the degree to which salmon are opportunistic feeders needs to be better established. Nevertheless, the results of my research emphasize the importance of further investigation into a carrying capacity. An opportunity exists to study more fully the impact that juvenile salmon have on their food resources.

The use of a computer program that modelled hatchery release manipulation experiments in the Georgia Strait provided some insight into the potential outcomes of such an experiment. The most significant conclusion to be drawn from this gaming is an indication of the need for very long-term hatchery manipulations. Even with 75% reductions in hatchery releases every second year, the model suggests that an experiment may take as long as 14 years to prove that a carrying capacity limit is impacting coho stocks. For chinook, the same result could take twice as long.

However, if such an experiment is undertaken, the model offers some ways to make it as efficient as possible. Firstly, greater fluctuations in hatchery releases provide more statistical contrast. This makes the pattern of results easier to interpret. Secondly, it appears that current exploitation rates of the chinook and coho stock may be close to the ideal levels for providing insight via such an experiment. Therefore, if the results of the experiment take precedence over rebuilding failing stocks, then fishing levels should be neither increased or decreased during the course of the trial. The most important implication of this result is the fact that concurrent attempts to rebuild stocks through other means will prolong the length of time an experiment takes to show conclusive results.

It remains to be seen whether or not the need to understand carrying capacity impacts in the Georgia Strait becomes great enough to overcome the economic factors supporting the operation of hatchery programs. It can only be hoped that further investigations, whatever form they take, provide the necessary information in time to reverse the current declines in salmon stocks.

## REFERENCES

- Anderson, E.P., I.K. Birtwell, S.C. Byers, A.V. Hincks, and G.W. O'Connell. 1981. Environmental effects of harbour construction activities at Steveston, British Columbia. Part 1. Main Report. Can. Tech. Rep. Fish. Aquat. Sci. 1070: vii + 153 p.
- Bartell, S.M., J.E. Breck, R.H. Gardner, and A.L. Brenkert. 1986. Individual parameter perturbation and error analysis of fish bioenergetics models. Can. J. Fish. Aquat. Sci. 43: 160-168.
- Boisclair, D., and Leggett, W.C. 1989. The importance of activity in bioenergetics models applied to actively foraging fishes. Can. J. Fish. Aquat. Sci. 46: 1859-1867.
- Bowden, J. and Johnson, C.G. 1976. Migrating and other terrestrial insects at sea. In: Marine Insects. L. Cheng. American Elsevier Publishing Company, Inc. New York, N.Y. pp. 97-117.
- Bradford, M.J. 1995. Comparative review of Pacific salmon survival rates. Can. J. Fish. Aquat. Sci. 52: 1327-1338.
- Brodeur, R.D. 1989. Neustonic feeding by juvenile salmonids in coastal waters of the Northeast Pacific. Can. J. Zool. 67: 1995-2007.
- Brodeur, R.D., R.C. Francis, and W.G. Pearcy. 1992. Food consumption of juvenile coho (*Oncorhynchus kisutch*) and chinook salmon (*O. tshawytscha*) on the continental shelf off Washington and Oregon. Can. J. Fish. Aquat. Sci. 49: 1670-1685.
- Brodeur, R.D., H.V. Lorz, and W.G. Pearcy. 1987. Food habits and dietary variability of pelagic nekton off Oregon and Washington, 1979-1984. NOAA Tech. Rep. 46: 85 p.
- Brodeur, R.D., and W.G. Pearcy. 1992. Effects of environmental variability on trophic interactions and food web structure in a pelagic upwelling ecosystem. Mar. Ecol. Prog. Ser. 84: 101-119.
- Brodeur, R.D., W.G. Pearcy, B.C. Mundy, R.W. Wisseman. 1987. The neustonic fauna in coastal waters of the northeast Pacific: abundance, distribution, and utilization by juvenile salmonids. Oregon state university Sea Grant College Program. Corvallis, Or. ORESU-T-87-001.
- Brown, T.J., C.D. McAllister, and B.A. Kask. 1987. Plankton samples in Campbell River and Discovery Passage in relation to juvenile chinook diets. Can. MS. Rep. Fish. Aquat. Sci. 1915: 35 p.
- Cheng, L. 1975. Marine pleuston - animals at the air sea interface. Oceanogr. Mar. Biol. Annu. Rev. 13: 181-212.
- Clifford, P.J., W.P. Cochlan, P.J. Harrison, K. Yin, M.J. Sibbald, L.J. Albright, M.A. St. John, and P.A. Thompson. 1989. Plankton production and nutrient dynamics in the Fraser River Plume, 1987. UBC Dept. Ocean. MS Rep. 51: 116 p.
- Clifford, P.J., P.J. Harrison, M.A. St. John, K. Yin, and L.J. Albright. 1991. Plankton production and nutrient dynamics in the Fraser River Plume, 1989. UBC Dept. Ocean. MS Rep. 54: 213 p.
- Cross, C.L., L. Lapi, and E.A. Perry. 1991. Production of chinook and coho salmon from British Columbia hatcheries, 1971 through 1989. Can. Tech. Rep. Fish. Aquat. Sci. 1816: 48 p.

- Cummins, K.W., and J.C. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. *Mitt. Int. Theor. Agnew. Limnol.* 18: 158 pp.
- DFO. 1992 a. Industry Report. Can. Dept. of Fisheries and Oceans, Pacific Region. 10 p.
- DFO. 1992 b. Strait of Georgia coho salmon planning process and recommendations; south coast coho initiative final report. Can. Dept. of Fisheries and Oceans, Pacific Region, manuscript report. 54 p.
- Foskett, D.R. 1951. Young salmon in the Nanaimo area. *Progr. Rep. of the Pac. Cst. Stns.* 85:18.
- Fraser, F.J., E.A. Perry and D.T. Lightly. 1983. Big Qualicum River salmon development project. Volume 1: a biological assessment 1959-1972. *Can. Tech. Rep. Fish. Aquat. Sci.* 1189: 198 p.
- Graham, C.C., and A.W. Argue. 1972. Basic data on Pacific salmon stomach contents, size, catch and effort for 1967 and 1968 test trolling catches in Juan de Fuca Strait, British Columbia. *Can. Fish. Serv. Man. Rep.* 6: 405 p.
- Harrison, P.J., J.D. Fulton, F.J.R. Taylor, and T.R. Parsons. 1983. Review of the biological oceanography of the Strait of Georgia: pelagic environment. *Can. J. Fish. Aquat. Sci.* 40: 1064-1094.
- Healey, M.C. 1978. The distribution, abundance, and feeding habits of juvenile Pacific salmon in Georgia Strait, British Columbia. *Fish. Mar. Serv. Tech. Rep.* 788: 49 p.
- Healey, M.C. 1980. The ecology of juvenile salmon in Georgia Strait, British Columbia. In: Salmonid Ecosystems of the North Pacific. W.J. McNeil and D.C. Himsworth. Oregon State University Press and Oregon State University SeaGrant College Program. Corvallis, Oregon. 203-229.
- Healey, M.C. 1991. Life History of chinook salmon (*Oncorhynchus tshawytscha*). Chapter in: Pacific salmon life histories. C. Groot and L. Margolis. UBC Press. Vancouver, B.C. pp 313-393.
- Henry, K.A. 1978. Estimating natural and fishing mortalities of chinook salmon, *Oncorhynchus tshawytscha*, in the ocean, based on recoveries of marked fish. *Fish. Bull. (U.S.)* 76: 45-57.
- Hewett, S.W., and B.L. Johnson. 1992. Fish bioenergetics model 2. University of Wisconsin Sea Grant Institute. WI.
- Hilborn, R. and C.J. Walters. 1992. Quantitative fisheries stock assessment: choice, dynamics, and uncertainty. Routledge, Chapman and Hall. New York, N.Y. pp 349-368.
- Hinch, S. 1996. Personal communication.
- Holtby, L.B. 1988. Effects of logging on stream temperatures in Carnation Creek, British Columbia, and associated impacts on the coho salmon (*Oncorhynchus kisutch*). *Can. J. of Fish. Aquat. Sci.* 45: 502-515.
- Kitchell, J.F. 1983. Energetics. In Fish Biomechanics. P.W. Webb and D. Weihs. Praeger Scientific Publishers. New York, N.Y. pp. 312-338.
- Kitchell, J.F., D.J. Stewart, and D. Weininger. 1977. Applications of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum*). *J. Fish. Res. Board Can.* 34: 1922-1935.

- LeBrasseur, R.J. 1966. Stomach contents of salmon and steelhead trout in the northeastern Pacific Ocean. J. Fish. Res. Bd. Canada. 23(1): 85-100.
- Macdonald, J.S., I.K. Birtwell, and G.M. Kruzynski. 1987. Food and habitat utilization by juvenile salmonids in the Campbell River estuary. Can. J. Fish. Aquat. Sci. 44: 1233-1246.
- Manzer, J.I. 1968. Food of Pacific salmon and steelhead trout in the northeast Pacific Ocean. J. Fish. Res. Bd. Canada. 25(5): 1085-1089.
- Manzer, J.I. 1969. Stomach contents of juvenile Pacific salmon in Chatham Sound and adjacent waters. J. Fish. Res. Bd. Canada. 26: 2219-2223.
- Mathews, S.B., and R. Buckley. 1976. Marine mortality of Puget Sound coho salmon (*Oncorhynchus kisutch*). J. Fish. Res. Board Can. 33: 1677-1684.
- McGurk, M.D. 1996. Allometry of marine mortality of Pacific salmon. Fish. Bulletin. 94: 77-88.
- Myers, K.W. 1979. Comparative analysis of stomach contents of cultured and wild juvenile salmonids in Yaquina Bay, Oregon. In: Gutshop '78: fish food habits studies: proceedings of the Second Pacific Northwest Technical Workshop. S.J. Lipovsky and C.A. Simenstad (eds.) Wash. Sea Grant Publ. WSG-WO-79-1. pp. 155-162.
- Ney, J.J. 1990. Trophic economics in fisheries: assessment of demand-supply relationships between predators and prey. Rev. Aquat. Sci. 2: 55-81.
- Nickelson, T.E. 1986. Influence of upwelling, ocean temperature, and smolt abundance on marine survival of coho salmon (*Oncorhynchus kisutch*) in the Oregon Production Area. Can. J. Fish. Aquat. Sci. 43: 527-535.
- Parker, R.R. 1962. Estimations of ocean mortality rates for Pacific salmon (*Oncorhynchus*). J. Fish. Res. Board Can. 19: 561-589.
- Parker, R.R. and W. Kirkness. 1956. King salmon and the ocean troll fishery of southeastern Alaska. Alaska Dep. Fish. Res. Rep. 1: 64 p.
- Parkinson, E. 1995. Personal communication.
- Peterson, W.T., R.D. Brodeur, and W.G. Pearcy. 1982. Food habits of juvenile salmon in the Oregon coastal zone, June 1979. Fish. Bull. U.S. 80: 841-851.
- Prakash, A. 1962. Seasonal changes in feeding of coho and chinook (spring) salmon in southern British Columbia waters. J. Fish. Res. Bd. Canada. 19(5): 851-866.
- Ricker, W.E. 1976. Review of the rate of growth and mortality of Pacific salmon in salt water, and noncatch mortality caused by fishing. J. Fish. Res. Bd. Canada. 33: 1483-1524.
- Robinson, D.G. 1969. Data record; number, size composition, weight and food of larval and juvenile fish caught with a two-boat surface trawl in the Strait of Georgia July 4-6, 1967. Man. Rep. Fish. Res. Bd. of Canada. 1012: 32 pp.
- Rowan, D.J., and J.B. Rasmussen. 1996. Measuring the bioenergetic cost of fish activity in situ using a globally dispersed radiotracer (<sup>137</sup>Cs). Can. J. Fish. Aquat. Sci. 53 (in print).

- Sandercock, F.K. 1991 Life History of coho salmon (*Oncorhynchus kisutch*). Chapter in: Pacific salmon life histories. C. Groot and L. Margolis. UBC Press. Vancouver, B.C. pp 397-3445.
- Shannon, L.V. and J.G. Field. 1985. Are fish stocks foodlimited in the southern Benguela pelagic ecosystem? Mar. Ecol. Prog. Ser. 22: 7-19.
- Shapovalov, L., and A.C. Taft. 1954. The life histories of the steelhead rainbow trout (*Salmo gairdneri*) and silver salmon (*Oncorhynchus kisutch*) with special reference to Waddel Creek, California, and recommendations regarding their management. Calif. Dept. Fish Game Fish. Bull. 98: 375 p.
- Shenker, J.M. 1988. Oceanographic associations of neustonic larval and juvenile fishes and Dungeness crab megalopae off Oregon, 1984. Fish. Bull. U.S. 86: 299-317.
- St. John, M.A., J.S. MacDonald, P.J. Harrison, R.J. Beamish, E. Choromanski. 1992. The Fraser River plume: some preliminary observations on the distribution of juvenile salmon, herring, and their prey. Fish. Ocean. 1(2): 153-162.
- Stewart, D.J., J.F. Kitchell, and L.B. Crowder. 1981. Forage fishes and their salmonid predators in Lake Michigan. Trans. Amer. Fish Soc. 110: 751-763.
- Stewart, D.J., D. Weininger, D.V. Rottiers, and T.A. Edsall. 1983. An energetics model for lake trout, *Salvelinus namaycush*. Application to the lake Michigan population. Can. J. Fish. Aquat. Sci. 40: 681-698.
- Thompson, R.E. 1981. Oceanography of the British Columbia coast. Can. Spec. Publ. Fish. Aquat. Sci. 56: 291 pp.
- Thorntsen, K.W., and A.S. Lessem. 1978. A temperature algorithm for modifying biological rates. Trans. Amer. Fish. Soc. 107: 284-287.
- Walters, C.J. 1993. Where have all the Coho gone? Proceeding to : Coho workshop. 1992, Nanaimo, B.C. The Assoc. of Professional Biologists of B.C. 18 p.
- Walters, C.J. 1994. Use of gaming procedures in evaluation of management experiments. Can. J. Fish. Aquat. Sci. 51: 2705-2714.
- Walters, C.J. 1995. Personal communication.
- Walters, C.J., R. Hilborn, R.M. Peterman, and M.J. Staley. 1978. Model for examining early ocean limitation of Pacific salmon production. J. Fish. Res. Board Can. 35: 1303-1315.
- Walters, C.J., and D. Ludwig. 1994. Calculation of Bayes posterior probability distributions for key population parameters. Can. J. Fish. Aquat. Sci. 51: 713-722.
- Zaitsev, Y.P. 1970. Marine neustonology. Nauk Dumka, 264 pp. (in Russian, transl. Israel Program for Scientific Translation).