THE INFLUENCE OF NATURAL PREDATION
ON THE POPULATION DYNAMICS OF PACIFIC SALMON

An Experimental Study

by

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ABSTRACT

Predation is widely assumed to make an important contribution to the determination of year class strength in Pacific salmon. For the most part, this assumption is based on little in the way of a functional understanding of predator-prey interactions involving juvenile salmon. As a first step towards addressing this shortcoming, this thesis presents the results of a field experimental study that evaluates functionally the interaction between a predator, prickly sculpins (*Cottus asper*) and chum salmon fry (*Oncorhynchus keta*).

The field research was conducted at an estuarine (Fraser estuary) and a freshwater (Rosewall Creek) site. *In situ* enclosures were used to ascertain the effect of prey density, prey and predator size and alternate prey on sculpin predation rates. Field and laboratory observations of predator distribution, abundance and feeding behaviour were used to complement the enclosure experiments.

For the most part the experimental results were consistent with expectation. Predator search rates were far lower than expected, however; possibly due to partial spatial segregation of the predator from its prey. As well, the data did not fit a simple stochastic model of predation based on random search and encounter, suggesting that the predation process is far from random. Alternate prey strongly influenced predation on chum fry, as did predator size. Larger sculpins had greater search rates and maximum ration levels. In contrast, prey size did not appear to influence predation.

The experimental results were combined with other field data to develop crude estimates of the overall impact of sculpin predation on chum fry in the two systems studied. In the Fraser estuary, the impact estimates are particularly uncertain, due to inadequate knowledge of sculpin abundance and chum fry residence times. Nevertheless, plausible esti-
mates are high enough to be considered significant (6-81%). For Rosewall Creek, a simulation model was developed and used to explore the effect of changing fry production on sculpin predation rates. The key result was that although the model predicted compensatory mortality to occur as fry abundance increased, it was not sufficient to regulate the prey population.

An additional unexpected result of the field experiments was gorging of fry by sculpins at very high prey densities. This behaviour is not predicted by conventional predation models, although it has been observed in many predator-prey systems. Two alternative models are proposed that might account for this phenomenon, one based on digestive physiology and the other on optimal foraging theory. Evidence is presented to suggest that the former is unlikely to be true, while the latter may offer a realistic generalization of conventional predation models that accounts for extrinsic restrictions on the predator's foraging behaviour.
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INTRODUCTION

1.1 General Introduction

Mortality during the early life history of fishes has been the focus of a great deal of research during the past half century (Saville 1971, Blaxter 1974). Emphasis on early life stages owes its origins to the pioneering observations of Hjort (1914), who pointed out that year class strengths of many fish species seem to be established at an early age. One group of fishes that provide a particularly good example of this is the Pacific salmons (genus Oncorhynchus). Neave (1953) provided compelling evidence in support of Hjort's observations for pink (Oncorhynchus gorbuscha) and chum (O. keta) salmon, and similar evidence has been obtained for other species (e.g., Foerster 1968). If mortality acting on early life stages is playing a key role in determining year-class strengths, then a better understanding of the factors that influence this process should be of considerable value to the management and enhancement of salmon populations.

Not surprisingly, a large number of factors, both biotic and abiotic, have been considered as possible mortality agents that act on salmon during their early life. Predation is one such factor, and has often been cited as a controlling factor in the population dynamics of a wide variety of organisms. Many authors have suggested that
predation is one of the most important sources of mortality in the early life of salmon (Foerster and Ricker 1941, Neave 1953, Parker 1968, 1971, Ward and Larkin 1964).

The study presented in this thesis was stimulated by these observations. It is a study of predation by a sculpin, Cottus asper, on chum salmon fry, in both freshwater and estuarine habitats. While predation has been the subject of numerous investigations of juvenile salmon, it is my contention that much scope remains for further research, especially in terms of linking empirical observations of predation with theoretical models. This has been the focus of the study, with experimental activities being designed to test predictions derived primarily from theory.

The remainder of this introduction focusses on two issues. First I will review the historical evidence that predation is an important source of mortality for juvenile salmon. In this discussion I will emphasize how most previous studies lack either the quantitative basis or the theoretical underpinnings to allow conclusions on the implications of predation to salmon population dynamics. Second, I will present a body of predation theory, based on the concepts of functional and numerical responses (Holling 1959b), which forms the theoretical basis for this study. Here, I will focus on how some of the predictions of these theoretical models might have important implications for salmon
management and especially enhancement.

The thesis is divided into eight chapters. In Chapter 2 I develop the predictions that the study was designed to test. Included in this chapter is the development of an alternative model of predation to those presented in the theoretical section of the introduction. Chapter 3 details the experimental methods used to test these predictions, including a description of the study areas where my field experiments were conducted. Chapters 4 and 5 present the major results of the study, emphasizing their implications regarding the predictions outlined in Chapter 2. Chapter 6 is devoted to a discussion of the population level consequences of prickly sculpin predation to chum salmon. In Chapter 7 I present and compare two additional models of predation that attempt to explain a result I obtained that cannot be accounted for by traditional predation models. Finally, Chapter 8 presents a brief summary of my overall conclusions.

1.2 Historical Evidence

Historical evidence for the importance of predation comes from a variety of sources, ranging from casual observation to detailed experimental studies. To emphasize the different approaches that have been taken to this problem, I have divided the literature into four classes of studies.
1.2.1 Qualitative Assessments of Predation

As might be expected, this category encompasses most of the literature concerned with predation on juvenile salmon. Due to their qualitative nature, such studies do little to evaluate the potential impact of predation. Their principal contribution is to emphasize the diversity of potential predators on salmon, and to point out how predation by any one predator species varies amongst systems.

A wide variety of fish and bird species have been reported in the literature as predators on juvenile salmon. Examples include sculpins of the genus *Cottus* (Roger 1971, Patten 1962) and *Leptocottus* (Dunford 1975), Arctic char (*Salvelinus alpinus* (Nelson 1966, Moriarity 1976), Dolly Varden (*S. malma*) (Armstrong 1970, Roos 1959), coho salmon smolts (*Oncorhynchus kisutch*) (Roos 1960), squawfish (*Ptychocheilus oregonense*) (Brett and McConnell 1950, Steigenberger 1966), herring (*Clupea harengus pallasi*) (Thorstenstein 1962), river lamprey (*Lampetra ayresi*) (Roos et al. 1973, Miller et al. 1967) and mergansers (*Mergus* sp.) (Senn 1961). That predation by a particular predator can vary considerably among systems is evidenced by a comparison of Dolly Varden predation on sockeye smolts in the Chignik system, Alaska (Narver and Dahlberg 1965, Roos 1959) and in southeastern Alaska (Armstrong 1970) or Lakelse Lake, B.C. (Brett and McConnell 1950). The incidence of predation was very low in the Chignik (~4.0%) but was high enough to be
considered significant (~50.0%) in the other systems.

Reports of the overall incidence of predation, however, can give a misleading picture of the importance of predators in a system. Incidence, which is normally measured as the proportion of predators sampled that were found to contain prey in their stomachs, ignores the abundance of the predator and its capacity for prey. An abundant predator with a large capacity for prey may have a large impact on a prey population, even though the observed incidence of predation is quite low.

The spatial and temporal scales over which overall incidence is measured can also give rise to misleading impressions. For example, Roos (1959) reports a low incidence of Dolly Varden predation on sockeye smolts in the Chignik system. His incidence figures, however, are averaged either over all areas considered or over the entire sampling season. If one reanalyses his data considering only the period of smolt outmigration and the narrow, fast flowing stream areas where prey are concentrated, one arrives at much higher incidence figures (40-60% instead of ~4%). Considering that Dolly Varden are abundant in this system and have the capacity to consume several smolts in a single feeding, they could well be an important source of mortality for sockeye salmon.
1.2.2 Quantitative Estimates of Predation Impact

Many authors have attempted to go beyond simply reporting the existence of predation. Bailey (1974) combined predator and prey population estimates with an assumed daily consumption per predator to arrive at an estimate of the overall predation rate* on seaward migrating pink and chum populations in the Fraser River. Patten (1967) actually measured consumption, but assumed that average stomach contents were equivalent to average daily consumption in estimating the losses of chinook fry to sculpin predators. Other authors incorporated a measure of predator digestion rates into their analyses, thus providing a more realistic estimate of average daily consumption (Foerster 1968, Hunter 1959, Semko 1954, Rogers et al. 1972).

A common feature of all these studies is that they explicitly deal with a dynamic situation in a static fashion. Prey and predator numbers will vary considerably during the entire period that predation is occurring; these variations are likely to influence the rates of predation (see section 1.3 below). So long as the estimates of consumption rates and predator numbers are averaged over the entire period, the impact estimates should be accurate. If,

*The expression "predation rate" is intended here and throughout this thesis to refer to the rate of mortality (i.e., percent or proportion killed) imposed by predation. Other expressions (e.g., consumption rates, number of successful attacks) will be used to refer to the number eaten or killed by individual predators.
on the other hand, consumption rates were only measured at certain times during the prey migration, significant errors in the estimated impact could be obtained. For instance, measures of consumption near the peak of the migration will probably overestimate the numbers consumed near the beginning and end of this period.

Cameron (1958), Hunter (1959) and MacDonald (in Foerster 1968, p. 155) avoided this potential problem by attempting to measure predation impact directly. They released marked fry in a stream containing other emerging fry and recaptured these fry at a downstream weir. The proportion of marked fish that were recaptured was used together with counts of unmarked fry to estimate the mortality of fry in that section of stream. They estimated mortality rates to be on the order of 50-90%. In addition to the usual problems associated with increased susceptibility of marked fish to predation due to the marking process, there is a problem with the specific experimental design of these studies. The estimation procedure which calculates the mortality rates assumes that marked and unmarked fish were subject to the same predation pressure. However, spawning (and thus emergence of fry) occurred throughout the stream while all marked fish were released at a single point. If predation is related to the distance a prey organism has to travel through a predator "gauntlet", then this assumption could quite easily be seriously violated.
1.2.3 Predator Removal Experiments

Another indirect but effective way of evaluating the impact of predators on a population is to selectively remove predators and see if the prey population responds. Foerster and Ricker (1941), in their extensive studies of Cultus Lake sockeye production, undertook a predator removal experiment which yielded a 300% increase in sockeye survival for three years. Elson (1962) observed increases of 200-400% in Atlantic salmon (*Salmo salar*) smolt production resulting from active control of bird (especially merganser) predation. Currently, a program is underway in the Wood River system in Alaska to control Arctic char predation on sockeye smolts by capturing the char and holding them in anchored cages during the seaward migration of the smolts (Meacham and Clark 1978). Predator control experiments, where possible, appear to offer potentially great rewards.

1.2.4 Functional Approaches

The studies described above were largely concerned with estimation of aggregate mortality rates due to predation. No attempt was made to establish a functional relationship between predation rates and some other variable (biotic or abiotic) that might provide a basis for extrapolation to other situations. While aggregate studies (at least the quantitative ones) may provide good evidence for the importance of predation in a particular system at a particular
time, they do not provide a functional basis for prediction at other places or times. The fact that the observational studies indicate different responses for the same predator-prey combination in different systems, suggests that extrapolation without functional information may be unwise.

Studies which have taken a functional or behavioural approach to predation are much less common. Patten (1971) showed that light intensity influenced predation rate (three times as great on moonlit nights as on dark nights). Similarly, Ginetz (1972) and Ginetz and Larkin (1976) considered light, turbidity and water velocity as factors which influence rainbow trout (Salmo gairdneri) predation on sockeye fry. Coutant (1973) demonstrated increased susceptibility of thermally shocked chinook fry to trout predation.

One factor generally accepted to play a major role in determining predation rates is prey size. The assumption of size selective predation on juvenile salmon often forms a critical component of simulation models of salmon populations (Walters et al. 1978, Belford 1978). Three authors have attempted to measure size selection by coho smolts feeding on juvenile salmon fry in aquaria, and found that smaller prey were selected (Parker 1971, Beall 1974, Walker 1974). Beall also looked at prickly sculpin predation, and found no evidence of size selection. More recently, Hargreaves and LeBrasseur (1985) re-examined Parker's (1971) data and also conducted a series of field enclosure experi-
ments in which coho smolts were offered pink and chum fry of contrasting sizes. They concluded that species selection (pinks preferred over chums) offered a more plausible explanation than size selection for both their results and Parker's and that the latter was of minimal importance in determining prey selection. They did not speculate on what differences between pinks and chums might be responsible for this species selection, but noted that no spatial segregation occurred.

Of the factors that can potentially affect a predator-prey interaction, two are fundamental to all interactions. These two are prey density and predator density. Despite this fact, only three studies have been reported in which the effect of either factor on predation rates was explicitly considered (Ricker 1941, Ginetz 1970, Peterman and Gatto 1978); in all these cases prey density was the independent variable.

1.3 Theoretical Considerations

The evidence presented in the previous section, especially that obtained from mark-release and predator removal studies, demonstrates that predation can be a major source of mortality for juvenile salmon. Presently, considerable effort is being directed towards the enhancement of salmon stocks, mostly by increasing fry production with the goal of increasing returns to sport and commercial fisheries. For
the enhancement programs to be successful, predation on salmon fry must not increase in a manner that compensates for the increased fry production. To identify the circumstances under which this undesirable situation might obtain, it is necessary to consider the theory of predator-prey interactions.

Predation theory owes its origin to the well-known Lotka-Volterra (Lotka 1925, Volterra 1928) and Nicholson-Bailey (Nicholson and Bailey 1935) models of predator-prey population dynamics. Today these models are valued more for their historical significance and mathematical properties than for their merits as realistic descriptions of natural processes. Their most significant weakness is that they assume predation rates are independent of both predator and prey densities.

Solomon (1949) recognized this limitation, and introduced the concepts of functional and numerical responses. Both refer to predator responses to changes in prey density; the former describes how an individual predator's attack rate is affected, while the latter considers changes in the predator population size. Both responses are implicit in the early predation models, which assume each to be linear functions of prey density for all prey densities. The most important step was to recognize that non-linear responses are more likely in natural situations.

Recognition of this fact, and a consideration of its
implications to population dynamics, formed the basis of the now classic studies of predation by Holling (1959a,b,1965,1966). Holling added a third component to Solomon's original two: the response of predators to their own density (the "competition response"), as it affects predation rates. He argued convincingly that the key to a realistic model of predation was a thorough understanding of the nature of each of these three components. Most of Holling's work was devoted to the functional response. I will begin by discussing this component, since it is also the focus of the study presented here. Later, I will briefly outline some relevant theory concerning the other components.

1.3.1 Functional Response

Holling argued that the most effective way to analyze a process is to divide it into a number of components and study each independently, but in the context of the integrated process (Holling 1963). Some of these components may be considered as basic to all manifestations of the process, while others are only present in some cases. Holling's first model of predation (Holling 1959b) was developed by considering only those components which he identified as basic to the functional response. These are the rate of effective search of the predator (the effective area or volume searched per unit time by the predator), the time prey are exposed to predation and the time a predator spends
handling individual prey. By assuming that each of these components is constant under all circumstances Holling derived the well known "disc equation":

\[ N_a = \frac{a \cdot N \cdot T_t}{1 + a \cdot h \cdot N_o} \]  

(1)

where \( N_a \) = total number of prey eaten; 
\( a \) = rate of effective search; 
\( N_o \) = prey density; 
\( h \) = handling time per prey item; and 
\( T_t \) = total time prey exposed to predation.

This can be considered the basic functional response model. It predicts that consumption will increase continuously to an asymptote as prey density increases, with a monotonically decreasing slope. The rate of increase (initial slope) is determined by the "a" parameter while the asymptote is given by the ratio \( T_t / h \).

In virtually any natural situation, the assumption that these components are constant is likely to be violated. In particular, the components themselves may vary in response to changes in prey density, either directly or through the action of subsidiary components such as learning and hunger. Holling (1965) demonstrated that the presence of these subsidiary components can give rise to four possible functional response forms (Figure 1), of which one (Type II) is described by the disc equation.

The form of the functional response can have important
Figure 1. The four possible functional response types, as proposed by Holling (1965). Shown are the number of attacks versus prey density (a) and the predation rate versus prey density (b).
implications to the population dynamics of the prey (see section 1.3.4 below). Examples of each form can be found in the literature (see Holling 1965, 1966, Murdoch and Oaten 1975, Hassell 1978, for reviews). Holling predicted that Type II responses would be typical of invertebrates while the sigmoid Type III response would be more common among vertebrate predators. More recent evidence (Hassell et al. 1977) suggests that many invertebrates may also have Type III responses. Type III responses are found whenever the rate of successful search increases as prey density increases. The most commonly cited cause of this increase is predator learning, as manifested by phenomena such as "search image formation" (Tinbergen 1960) and "switching" (Murdoch 1969). Type I and IV responses are less commonly seen, but are expected for predators whose handling time is short until a maximum consumption rate is reached, after which feeding ceases (Type I), or whose feeding is inhibited by very high prey densities (Type IV).

Two simple mathematical models have been developed which are capable of describing each of the four response types*, given the appropriate choice of parameters. Both have been derived from the disc equation, by incorporating an expression describing changes in search rates as prey density changes. The first (Hassell et al. 1977) uses an

*Strictly speaking, the Type I response cannot be described by a continuous model. Responses which approach the Type I form can be obtained from these models, however.
expression identical to the disc equation to predict variation in the rate of effective search, \( a \), with prey density, \( N_0 \):

\[
a = \frac{b \cdot N_0}{1 + c \cdot N_0}
\]  

(2)

Substituting (2) into (1) gives

\[
N_a = \frac{b \cdot N_0^2 \cdot T}{1 + c \cdot N_0 + b \cdot h \cdot N_0^2}
\]

(3)

Fujii et al. (1978) independently derived an alternative model in which search rates were assumed to increase exponentially with increasing prey density:

\[
a = a' \cdot \exp(c \cdot N_0)
\]

(4)

Substituting this expression into the disc equation, in its Michaelis-Menton form, gives

\[
N_a = \frac{A_{\text{max}} \cdot N_0 \cdot T}{g \cdot \exp(-c \cdot N_0) + N_0}
\]

(5)

These models can be fitted to functional response data, using non-linear estimation procedures. The best-fit parameter estimates provide a quantitative assessment of the form of the functional response. As well, the fitted model can be incorporated into models representing the population dynamics of the prey, thus allowing an evaluation of the population level consequences of predation.
1.3.2 **Competition Response**

The competition response (i.e., the response of predators to their own density) consists of two separate processes: exploitation (one predator's consumption reduces the prey remaining for others) and interference (one predator's presence inhibits, in some fashion, the feeding of another). Models have been developed to combine each of these processes with the functional response (exploitation: Griffiths and Holling 1969, Rogers 1972; interference: Watt 1959, Hassell and Varley 1969, Beddington 1975), mostly based on studies of arthropods. Mace (1983) recently reviewed the literature on models of exploitation and interference, and developed general models of the functional response which incorporate both processes. Both of these processes have the effect of reducing the success of individual predators. The effect of ignoring the competition response will thus be to overestimate the impact of predators on their prey, particularly if the predators are abundant and the prey is scarce.

1.3.3 **Numerical Response**

Predator numbers can vary in response to prey density on two very different time scales. In the short term, predators may aggregate in areas of high prey density (Hassell and May 1974). In the long term, high prey densities may result in greater survival and reproductive success of the
predator (and therefore increased numbers in future generations (Beddington et al. 1976). Related to this is the developmental response (Murdoch 1971), which concerns the effect of prey density on predator growth rates. Faster growth rates may feed back into higher predation rates, since larger predators often search faster or more efficiently and can consume greater numbers of prey.

The numerical response is perhaps the least well understood component of predator-prey interactions. Again, most of the research in this area has focussed on insects and other invertebrates. However, there are exceptions (e.g., Goss-Custard 1970, Smith and Dawkins 1971), including a recent study of the aggregation responses of mergansers to salmon smolts (Wood 1984). More often, the spatial (aggregation) and temporal (reproductive, developmental) requirements of such studies pose severe limitations to research on larger, longer lived animals.

1.3.4 Population Level Consequences

Numerous authors have considered the population level consequences of predator-prey interactions (e.g., Holling 1959b, Hassell and May 1973, Murdoch and Oaten 1975, Bazykin 1975), some even with a specific focus on fish populations (Ricker 1954, Beverton and Holt 1957). The key issue addressed by these studies concerns the circumstances under which predators are able to regulate the abundance of their
prey. For predation to have a stabilizing effect, predation rates must increase as prey density increases across some range of prey abundance. This type of mortality has been termed compensatory. Neave (1953) coined the term "depensation" to account for situations in which mortality rates decrease as prey density increases. Depensatory mortality is clearly destabilizing, since as prey get more abundant, mortality rates go down, giving rise to a positive feedback situation.

The ability of predators to regulate the abundance of their prey depends on the combined effect of their functional, competition and numerical responses. So long as the form of this "total" response is such that its slope decreases as prey density rises, the impact of predation will be depensatory. Considering only the functional response, this is the case for all prey densities given a Type II or IV form (Figure 1). Type I responses imply density independent mortality up to the threshold and depensatory mortality above.

Depensatory mortality has been predicted and observed in Pacific salmon populations (Neave 1953, Ricker 1954, Hunter 1959). Ward and Larkin (1964) proposed depensatory predation mortality together with a numerical response by rainbow trout to be responsible for the maintenance of quadrennial cycles in Adams River sockeye salmon. If the predator population is large enough relative to the productivity
of the prey, a stock size threshold will exist below which
the stock will collapse. The presence of such a threshold
may have important management implications (Clark 1976, Reed
1978).

Type III functional responses, on the other hand, have
a threshold prey density (the inflection point of the curve)
below which compensatory mortality occurs. Murdoch and Oaten
(1975) discuss a variety of mechanisms which allow predation
to contribute to population regulation, many of which act by
giving rise to a Type III functional response.

Peterman (1977) considered a simple population model in
which the population dynamics were determined by a Ricker
stock-recruitment curve (Ricker 1954) and a Type III func-
tional response. He showed that under such circumstances,
three equilibrium stock sizes could occur, two stable and
one unstable. The unstable equilibrium corresponds to the
stock collapse threshold discussed above, while the upper
stable state results from the compensatory mortality imposed
by the Ricker model. The lower stable state is a consequence
of the predator having a Type III total response.

Other components of predator-prey interactions may also
affect stability. For instance, time lags in the numerical
(reproductive) response tend to be destabilizing, while pre-
dator aggregation in areas of high prey density may impart
stability (Hassell and May 1974).
The compensatory mortality that can result from predation may also have important implications for the enhancement of salmon fry production. If predators on salmon are currently operating in the compensatory range of their total responses, then increases in fry output due to enhancement will not have the desired effect, due to compensatory increases in predation. If, on the other hand, predation is depensatory, enhancement activities will be further "enhanced" by reduced predation mortality.

In summary, there are both theoretical and empirical grounds for believing that predation has an important influence on the population dynamics of Pacific salmon. While considerable empirical information exists on the predators of salmon, little of this information is of use in assessing the population level consequences of their depredations. More precisely, very few of the existing studies of predation on juvenile salmon go further than identifying its presence or measuring its magnitude at a specific point in time. A better functional understanding of the the predator-prey interaction is badly needed if the role of predators in salmon population dynamics is to be realistically incorporated into management models. I maintain that this understanding can only be achieved by explicitly considering the key components of predation, namely the functional, competition and numerical responses.
The overall objective of this study was to examine the influence of natural predation on the dynamics of a fish population. To this end I selected a specific predator-prey interaction, prickly sculpins feeding on chum salmon fry, as the focus of a detailed field experimental study. The purpose of the study was thus to identify and quantify those factors that control sculpin predation. While little information already exists on prickly sculpin feeding, some inferences can be drawn from the literature. In this chapter, I examine this literature and derive a set of predictions that form the basis of my experimental design. First I consider the functional response, including its basic components as identified in Chapter 1. Then I examine the competition and numerical responses, and finally additional factors that may be subsidiary to the functional response.

2.1 Prickly Sculpin Functional Response

2.1.1 Qualitative Form of the Response

The central question concerning the form of the functional response is whether it is sigmoid (Type III) in shape. If not, then the predator's functional response will not contribute to compensatory mortality and thus to the regulation of prey abundance. Type III functional responses were initially associated with vertebrates (Holling 1965), particularly when a predator was given a choice of prey.
Since Holling's early work, this response form has been shown to be more widespread (Hassell et al. 1977) than first suggested, and does not appear to require the presence of alternate prey (Murdoch 1973 Hassell et al. 1976). Hassell et al. (1977) suggest that the Type II responses observed in earlier studies may have been artifacts of the experimental design. They showed that Type II responses will often be observed when highly preferred prey, or confined experimental arenas are used, even for predators which would otherwise exhibit Type III responses.

Among the numerous studies of functional responses, very few have considered fish as predators (Ivlev 1955, LeBrasseur et al. 1969); none prior to this study have looked at cottids, nor at fish preying on other fish. Thus it is difficult to draw any direct inferences from previous studies about the form of the response. Several studies have looked at the feeding behaviour and learning abilities of various fish species (e.g., Murdoch et al. 1975), and these would indicate that many species are indeed capable of "switching" and learning to exploit certain prey more efficiently with experience.

Prickly sculpins are generally considered to be sluggish bottom dwelling fish, relying primarily upon benthic invertebrates (mostly insects in fresh water, crustaceans in estuaries) as food. Salmon fry would appear to form only an incidental component of their diet except when sculpins find
themselves in areas of very high fry densities (Hunter 1959). This would suggest that salmon fry are not a highly preferred prey of sculpins, or at least that other prey are also considered quite acceptable. According to the arguments of Hassell et al. (1977), one would expect to observe a Type III response for prickly sculpins feeding on salmon fry, provided alternate prey were available. In the absence of alternate prey, a Type III response might still be observed due to learning effects, particularly for naive sculpins.

2.1.2 Rate of Effective Search

The rate of effective search determines the proportion of all the available prey in an area which are attacked by a predator in a given amount of time spent searching. If it is assumed that the number of prey encounters made in a given period of time can be considered a Poisson process* then it follows (Charnov and Orians 1973, Pulliam 1974) that the rate of effective search is given by the product of volume (or area) searched by the predator per unit time and the probability of prey capture once an encounter is made. Thus to estimate the rate of effective search, information is needed on predator and prey rates of movement, predator reactive distances and capture success.

*This assumption is easily justified if successive encounters are independent of each other (i.e., the prey are randomly distributed).
It is generally believed that sculpins are ambush predators, relying on their prey to come to them, rather than the reverse. Their cryptic coloration, "bullheaded" morphology with protruding, dorsally located eyes and well developed branchiostegal apparatus all suggest an animal adapted to waiting motionlessly for prey to approach nearby and then rapidly striking and capturing its quarry with a minimum of pursuit. This being the case, it seems reasonable to assume three things:

1. Rates of encounter with prey depend only upon prey movement rates and the predator's reactive field.

2. The reactive field must be quite small since prey must be very close for an efficient strike, especially for mobile prey such as salmon fry.

3. Capture success is very high for nearby prey but falls off rapidly as strike distance increases.

The second and third assumptions here are closely related and are based, in turn, on the assumption that salmon fry are better swimmers than prickly sculpins and thus could escape any pursuit for which they had sufficient time to react.

**Rates of Movement of Prey**

Much research has been conducted on the swimming speeds of fish under a variety of conditions (review by Beamish...
1978). This work, however, has mainly focussed on swimming capacities, over both short (burst) and extended (prolonged) periods of time. This is particularly true for salmon, where the extensive research of J.R. Brett and his colleagues in the 1960's contributes most of our empirical knowledge about salmon swimming speeds. The principal impetus for this work was concern about the ability of salmon to cope with modified flow regimes in rivers resulting from hydroelectric development. Thus, the objective was to identify "critical" swimming speeds for various sized fish, above which they would not be able to maintain themselves in an equivalent current for extended periods of time.

The literature on foraging swimming speeds, where a fish has the opportunity to move at a variety of speeds, is much more scarce. Most work has been concerned with movements of larval clupeoid fishes (Rosenthal and Hempel 1970, Hunter 1972). These authors found that movement rates of one to two body lengths per second were typically observed for actively foraging fish. Ware (1978), on the basis of energetic and hydrodynamic concepts, developed a theoretical argument that the optimal foraging speed for larger fish should fall within a similar range. His definition of optimal was the speed which maximized the net rate of energy intake for a given concentration of prey.

Both of these approaches derived rates of movement for actively foraging fish (either searching for or handling
prey) at all times. This assumption seems reasonable for situations where food supply is limiting and is therefore the overriding concern of the fish. Such a situation is quite probable for larval clupeoids where it has been shown (e.g., Houde 1979) that natural food concentrations are often low enough to severely affect larval survival. When food is not limiting, however, other factors may come into play that influence prey movement rates. Since the probability of encounter with a predator will increase as prey movement rates increase, it seems likely that a well-fed prey organism will reduce its swimming speed, relative to that of an actively foraging fish.

Studies of juvenile salmon feeding and growth in the Fraser and Nanaimo estuaries (Levy et al. 1979, Healey 1979, 1980) suggest that the food supply is not a limiting factor in these areas: both chum and chinook fry grow very rapidly during their period of estuarine residence. Therefore, if one to two body lengths per second is a reasonable swimming speed for an actively foraging fish, this figure likely provides an upper limit for juvenile salmon, at least in estuarine habitats.

**Predator Reactive Field**

There is no feeding behaviour literature on prickly sculpins. A number of authors have observed the feeding of closely related species in laboratory environments, however,
(Western 1969, Smyly 1957, Phillips and Claire 1966). These observations provide a basis for considering the range of possible reactive distances for prickly sculpins.

It is obvious from a sculpin's morphology that it is not adapted for an actively searching, pelagic form of life. The flattened body, particularly in the anterior region, and the absence of a swim bladder point to this conclusion. Also, most studies of cottid feeding behaviour emphasize a strong preference for moving prey. In spite of this immobility of the predator, its reactive field will depend critically on whether it is capable of stalking prey from a distance, or relies entirely upon ambushing closely approaching prey.

Western (1969) and Smyly (1957) observed both *Cottus gobio* and *Parenophrys bubalis* (first author only) to employ a stalking mode upon sighting prey. On the other hand, observations of *C. perplexus* (Phillips and Claire 1966) were quite different:

"They did not attempt to chase their prey, but instead would wait on the bottom until the fry swam over them. The sculpin would then lunge forward by utilizing the pectoral fins and then make the capture."

A key difference between these observations and those of the former two authors concerns the type of prey. Phillips and Claire considered salmonid fry while Smyly and Western mainly used invertebrates; possibly the fry were more wary
and better able to escape a sculpin attack from a distance.

In any event, both modes of behaviour have been observed in sculpins other than *Cottus asper*. Western observed reactive distances of up to 30 cm for sculpins preying on blowfly larvae, although he provided no information on the light conditions or the size of the prey. As a first approximation, however, this figure would seem to be reasonable as an estimate of the maximum distance from which prey are stalked. On the other hand, a sculpin relying entirely upon ambush would likely only have a reactive distance of approximately two to four centimeters.

A key consideration in view of these two extremes is that factors affecting the visibility of prey (e.g., light, turbidity, prey size) will have a substantial impact on the reactive distance of a stalking predator but little, if any, impact on an ambush predator. In fact, at the close quarters implied by ambush predation, non-visual stimuli (e.g., tactile, chemical) may play important roles in eliciting an attack.

**Capture Success**

Capture success once pursuit has been initiated has not been considered in the cottids, except for Western (1969) who observed *C. gobio* to have relatively little success at capturing prey in midwater. He attributed this to the fact that "...*C. gobio* is a clumsy swimmer...", and
pointed out that success was far greater when bottom feeding was employed.

It is reasonable to hypothesize that capture success will be less for a stalking predator than for an ambush predator, particularly when feeding on wary and active prey. Moreover, it seems likely that capture success will decrease as the length (i.e., distance) of pursuit increases since the prey will have more time to react to the predator's movement. Anyone who has observed salmon fry in aquaria or streams is aware that they are extremely sensitive to sudden movements.

It is difficult to develop plausible predictions of capture success, and how it is affected by reactive distance. However, it is worth pointing out that any tendency for capture success to decrease with increasing reactive distance will tend to offset increases in the rate of effective search due to stalking rather than ambushing. Proponents of the notion that animals always forage optimally in terms of maximizing some net benefit (i.e., energy intake) will argue that the observed feeding behaviour of sculpins should represent a compromise between these two opposing factors.

**Overall Rate of Effective Search**

The overall rate of effective search of a stationary,
bottom dwelling predator is given by:

\[ a = v \cdot r \cdot p_c \]  

where \( a \) = rate of effective search (m/hr); 
\( v \) = prey movement rate (m/hr); 
\( r \) = predator reactive distance (m); and 
\( p_c \) = probability of prey capture, given an encounter.

Even though the information discussed above does not provide a precise quantitative basis for predicting "a", it does allow me to bound the prediction. For a 35 mm chum fry, "v" should approximate 63-252 m/hr (.5-2. body lengths per second). Reactive distances for an ambush predator should be at least .03 m, as opposed to .30 m for a stalking predator. Capture success should be high (.8-1.) for ambush, and very low (.05-.1) for stalking. Applying these estimates to equation (6) gives rates of effective search of 1.51-7.56 m²/hr for an ambush predator, and 0.95-7.56 m²/hr for a stalking predator. Note that these estimates are based on a two-dimensional model of predation, which assumes that the prey are always close enough to the bottom to be within the predator's reactive field.

2.1.3 Handling Time

When Holling originally developed the disc equation, he pointed out that the existence of a finite handling time was the primary reason that predation rates cannot increase
indefinitely with prey density. It is handling time that causes the disc equation to have an asymptote. He also pointed out, however, that other factors such as hunger can influence the functional response. In his study of mantid predation (Holling 1966) he demonstrated a functional response qualitatively similar to a Type II response when hunger effects were explicitly considered. If a disc equation were fitted to the mantid response the estimate of the h parameter would not truly reflect handling time (since the latter was not constant), but would rather be indicative of the maximum possible ration of the predator during the experimental period. This is most easily shown by expressing the disc equation in Michaelis-Menton form:

\[ N_a = \frac{(T_t/h) \cdot N_0}{(1/(a \cdot h)) + N_0} \]  

(1)

Here, \( T_t/h \) gives the asymptotic value of \( N_a \), as \( N_0 \) gets large.

To understand the population level impacts of predation it is critical to know the value of the asymptote of the response and at what prey density it is approached. This determines how easily the prey population will be able to escape significant predation mortality by swamping its predators. As the functional response approaches the asymptote predation rates decline (see Figure 1b), unless there is a significant numerical response that increases predator numbers. Thus the greater the prey density, the less likely
it becomes that any particular individual will be captured.

If the digestion rates of the predator are sufficiently slow, then the maximum ration for any period less than one day should be a constant. Many estimates have been obtained of the daily ration of a variety of fish species under ad libitum feeding regimes (for review see Kapoor et al. 1975) as a proportion of body weight; reported values usually range from 1-15%, with isolated observations of much higher proportions.

Smyly (1957) noted a maximum daily ration (total weight of stomach contents) of on the order of 6% for C. gobio less than 100 mm total length. A 100 mm C. asper weighs approximately 15 g, implying a maximum ration of 0.9 g (1-2 fry). In the Fraser estuary, sculpins commonly reach much greater sizes than this (150-170 mm total length), with an average weight of approximately 75 g. At 6%, the maximum ration would be 4.5 g (5-8 fry). Several authors, however, have found that the ratio of maximum ration to body size decreases with increasing body size (Hunt 1960, Baldwin 1956, Pandian 1967). In addition, activity has been observed to affect this proportion (Hunt 1960), and older cottids are generally less active (Western 1969). Thus, a value of 3% (2.5-4 fry) per day is more reasonable for these larger sculpins.
2.1.4 Time of Exposure

The third basic component of the functional response represents the time prey are exposed to predation ($T_t$). In most experimental studies of predator functional responses, it is implicitly assumed that this time is equal to the length of the experiment. Prey are assumed to be continuously available and predators are assumed to spend all their time either searching for, or handling prey. In natural situation, however, predators have other constraints on their behaviour (e.g., avoiding predation themselves) which may reduce the time available for feeding. As well, prey often undergo changes in distribution and behaviour on various time scales (diurnal, seasonal) which may affect their exposure to predation. Thus the time of exposure in a natural situation may be considerably less than the entire period over which predation is observed.

In the present context, sculpins are known to be prey to other species (e.g., herons, mergansers), while chum fry alter their behaviour substantially between day and night (schooling, feeding during the day; dispersed, not feeding at night). Nevertheless, in the experiments conducted as part of this study, I have assumed that $T_t$ is equal to the experiment length. If observed predation rates are lower than expected, then the validity of this assumption must be questioned. In any event, extrapolations of experimental results to a real situation must consider
whether $T_e$ differs from the former to the latter.

2.1.5 Alternative Functional Response Models

So far, all the discussions in this chapter have focussed on the functional response as it is represented by Holling's disc equation. While the disc equation and its relatives are arguably the most realistic available models of the functional response, their use as models for estimating the parameters discussed above may not be entirely appropriate in this study. As deterministic models, they are derived by assuming that the experiment involves a large number of events (encounters, attacks) over an observation period that spans (i.e., averages across) several natural predation cycles (e.g., feeding-satiation-digestive pause-feeding, etc). For practical reasons (see Chapter 3) my experiments never extended beyond a single day. Given the small capacity of sculpins for chum fry (< 5 prey per feeding) and the fact that gut evacuation rates are unlikely to be sufficiently great to allow more than a single feeding to satiation in one day, these assumptions are expected to be violated in this study. This does not imply that the disc equation models are incorrect, but rather that the data collected in this study, if fitted to these models, may produce biased parameter estimates. For situations such as this, a stochastic model of predation is more appropriate.

Several authors have developed stochastic models of
predation (Charnov and Orians 1973, Curry and deMichele 1974, Sjoberg 1980), based on the principles of queuing or renewal theory. All of these models turn out to be identical to the disc equation when integrated over long time periods, and when random search is assumed. They all assume a constant handling time or digestive pause after each attack, an assumption which I contend is inappropriate for this study. Within a single predation cycle, one would expect a hungry predator to resume searching very shortly after consuming a single prey item, while a nearly sated predator may remain in a state of digestive pause for a considerable period of time.

For these reasons, I decided to consider an alternative model of predation, which does not have these limitations. The model I have chosen is derived by analogy from a very simple, state dependent, birth process model (Chiang 1968). In the analogy, the population, whose numbers are being modified by a birth process, is the population of salmon fry in a prickly sculpin stomach. A "birth" in this system results from the consumption of a single prey item. For the sake of completeness, a "death" process should also be defined which represents digestion of prey. Incorporation of digestion would add considerable complexity to the model, however, and since it is not expected to play a significant role on the time scale of the experiments in this study, I have chosen not to include it. Satiation is accounted for by allowing the birth rates (i.e., predator feeding rates)
to be state dependent; that is, as the population of prey in the predator's stomach increases, its rate of feeding decreases, eventually reaching zero at some carrying capacity (i.e., gut capacity). This approach allows the model to account for the effect of hunger on predator feeding rates, and does not require that handling times be held constant.

Since this is a stochastic model, it is possible to explicitly describe the probability of being in a given state (of stomach fullness), as well as the expected state (the mean), for any given prey density and experiment length. The probability of being in a given state, \( k \), after a short period of time, \( \Delta \) is given by:

\[
p_k(t+\Delta) = p_k(t) \cdot (1 - \lambda_k \cdot \Delta) + p_{k-1}(t) \cdot \lambda_{k-1} \cdot \Delta + o(\Delta), \quad k > 0
\]

and

\[
p_k(t+\Delta) = p_k(t) \cdot (1 - \lambda_k \cdot \Delta) + o(\Delta), \quad k = 0
\]

where \( p_k(t) \) = probability of being in state \( k \) (\( k \) items in the gut) at time \( t \);

\( \lambda_k \) = birth (attack) rate when in state \( k \); and

\( o(\Delta) \) = a quantity which decreases more rapidly than \( \Delta \), as \( \Delta \) decreases, and which represents the probability of changing state more than once during time \( \Delta \).

These can be rearranged to give:

\[
\frac{p_k(t+\Delta) - p_k(t)}{\Delta} = -\lambda_k \cdot p_k(t) + \lambda_{k-1} \cdot p_{k-1}(t) + \frac{o(\Delta)}{\Delta}, \quad k > 0
\]

and

\[
\frac{p_k(t+\Delta) - p_k(t)}{\Delta} = -\lambda_k \cdot p_k(t) + \frac{o(\Delta)}{\Delta}, \quad k = 0
\]
Taking the limit as $\Delta$ approaches zero results in the pair of differential equations:

\[
\frac{dp_k(t)}{dt} = -\lambda_k \cdot p_k(t) + \lambda_{k-1} \cdot p_{k-1}(t) \quad , \quad k>0
\]

and

\[
\frac{dp_k(t)}{dt} = -\lambda_k \cdot p_k(t) \quad , \quad k=0
\]

which can be solved analytically to give:

\[
p_k(t) = (-1)^k \cdot \lambda_0 \cdots \lambda_{k-1} \cdot \sum_{i=0}^{k} \frac{\exp(-\lambda_i \cdot t)}{\prod_{j=0}^{i} (\lambda_i - \lambda_j)_{j \neq i}}
\]

The expected number of attacks is thus simply:

\[
E(k) = \sum_{k=0}^{\infty} k \cdot p_k(t)
\]

This model is capable of generating Type I, II and III functional responses, depending on the relative values of the $\lambda_k$, but not Type IV. Since $\lambda_k$ is the rate of attack for a given state $k$, it depends on the rate of effective search of the predator when in that state, and the prey density. I chose to assume that search was random, which implies that:

\[
\lambda_k = a_k \cdot N_0
\]
2.2 Other Factors Affecting Predation

2.2.1 Competition Response

Exploitation

Since the period of residence of chum fry in freshwater (Hunter 1959) and estuarine (Levy and Northcote 1982) habitats appears to be short, the opportunity for sculpins to deplete their prey in these systems is probably limited. On the other hand an abundant population of predators upstream may reduce the availability of fry for predation further downstream. In general, whenever the predator population is imposing moderately high mortality rates on their prey (i.e., > 10-20%) the effect of exploitation on the total functional response cannot be ignored. This is normally accomplished by integrating the functional response over changing prey densities (Royama 1972, Mace 1983). If the distribution of attacks is known then the effect of exploitation can be deduced from knowledge of the functional response.

In the experiments conducted in this study, I deliberately prevented prey densities from changing sufficiently during the course of an experiment to necessitate accounting for exploitation. When the population level consequences of predation are considered, however, the models used to assess predator impacts implicitly account for this component of the total response (Chapter 6).
Interference

Interference competition results from one predator inhibiting the ability of another to capture prey, by means other than exploitation. Normally, interference involves physical contact between predators. Therefore, one would not expect interference to be an important part of the total response for sculpins, since they appear to be stationary predators. On the other hand, interference could be important if there were a limited number of preferred ambush sites in a particular area. This possibility was not explored as part of this study.

2.2.2 Numerical Response

Since chum fry are only present in those habitats where sculpins are found for relatively short periods of time, it is unlikely that a long-term (i.e., reproductive) numerical response would exist for this predator-prey interaction. The time during which fry are present is also a period when other sources of food for sculpins (e.g., crustacean invertebrates) are relatively abundant. On the other hand, a short-term (aggregative) numerical response is possible, and may be of considerable importance. Several authors (e.g., Hunter 1959, Krejsa 1967, Mason and Machidori 1976) have observed migratory movements of sculpins coincident with fry migrations. The question remains whether these migrations are actually in response to movements of fry, or if they are
related to other sculpins activities, such as spawning.

2.2.3 Alternate Prey

To evaluate the importance of alternate prey, it is useful to consider a multiple prey species version of the disc equation (Charnov and Orians 1973, Murdoch 1973):

\[ N_a(i) = \frac{a(i) \cdot N_0(i) \cdot T_t}{1 + \sum_{j} a(j) \cdot h(j) \cdot N_0(j)} \] (13)

where the parameters are the same as those for the single species equation (1), and the "i" and "j" subscripts refer to different prey types.

The multi-species disc equation is basically the same as the single species version except that the time available for searching has been reduced by an amount equal to the time spent handling prey other than the species of interest. An implicit assumption of this model is that the relative abundance of alternate prey does affect the rate of effective search for a given prey species. In other words, the model assumes that the predator does not exhibit "switching".

Using this model it is possible to predict the effect of changes in alternate prey availability on the slope and asymptote of the functional response to salmon fry. Consider the case where there are only two types of prey (i.e., sal-
mon fry and "others"). Then

\[ N_{a(1)} = \frac{a(1) \cdot N_o(1) \cdot T_t}{1 + a(2) \cdot h(2) \cdot N_o(2) + a(1) \cdot h(1) \cdot N_o(1)} \] (14)

where salmon fry = 1, others = 2. As \( N(1) \) gets very small, the slope of this relationship (i.e., the apparent rate of search for salmon fry) is given by

\[ a'(1) = \frac{a(1)}{1 + a(2) \cdot h(2) \cdot N_o(2)} \] (15)

Clearly, when alternate prey are absent, \( a'(1) = a(1) \). Thus the effect of alternate prey is to reduce the apparent rate of search by a factor of

\[ \frac{1}{1 + a(2) \cdot h(2) \cdot N_o(2)} \]

An important implication of this result is that the proportional reduction in slope is independent of the magnitude of \( a(1) \). Figure 2 demonstrates the effect of alternate prey abundance on \( a'(1)/a(1) \) (i.e., the proportional reduction in slope as \( N_o(2) \) increases), for three combinations of \( a(2) \) and \( h(2) \) parameter values.

To consider the effect of alternate prey on the asymptote of the functional response, note that as \( N_o(i) \) becomes large, \( a(i) \cdot h(i) \cdot N_o(i) \) will dominate the sum in the denominator of the multi-species equation, so that it
Figure 2. Predicted effect of alternate prey density on the apparent rates of search ($a'$) for a principal prey item, measured relative to the rate observed in the absence of alternate prey.

1) $a(2) = 1.0; h(2) = 0.025$
2) $a(2) = 2.0; h(2) = 0.05$
3) $a(2) = 0.5; h(2) = 0.012$

($m^2\cdot hr^{-1}$); (hr)
reduces to

\[ N_a(i) = \frac{a(i) \cdot N_o(i) \cdot T_t}{a(i) \cdot N_o(i) \cdot h(i)} = \frac{T_t}{h(i)} \]  

(16)

This is exactly the same as the result obtained when only one prey species is considered; thus alternate prey are predicted to have no effect on the asymptote of the functional response.

2.2.4 Predator Size

The most obvious effect of predator size on the functional response is to increase the gut capacity of the predator. If size does not affect maximum ration \( R_m \) as a proportion of body weight, a linear relation between \( R_m \) and size (in units of weight) might be expected. However, it has already been pointed out that this proportion tends to decrease with body size. In a study of two species of marine teleosts, Pandian (1967) showed that the relationship between intake calculated as a proportion of body weight, and body weight, was approximately linear for all sizes of fish greater than 10 g. Leaving aside the obvious statistical problems with this kind of analysis and the fact that such a model would predict absurd consequences at body weights greater than the range considered (i.e., 0% rations), these results serve as a first approximation. In effect, Pandian's results suggest that over a range of sizes
(10-150 g), \( R_m \) is a quadratic function of body weight:

\[
R_m = \frac{T_c}{h} = (a + \beta \cdot W) \cdot W
\]  

(17)

Predator size may also influence the rate of effective search, since burst speeds increase with increasing body size (Beamish 1978). This may allow an increase in the distance from which prey are attacked or an increase in the success of an attack from a given distance. Apparently conflicting evidence comes from Western (1969), who pointed out that in the marine cottid, *Parenophrys bubalis*, larger individuals were less likely to attack from relatively great distances. This may simply reflect the increased experience of larger individuals, if long distance attacks have a very low probability of success.

Finally, predator size may also affect the impact of alternate prey on the functional response. Increases in predator size are commonly associated with increases in diet breadth (Werner 1974). A wide variety of carnivorous fishes are known to undergo a shift in diet from primarily plankton or benthos, to primarily fish as they grow larger. Western observed this to be the case for *P. bubalis* and other authors (e.g., Patten 1977) have noted similar patterns in other cottid species. Assuming that prey abundance is actually indicative of prey availability, then changes in observed preference* should be related to changes in the

* here preference is defined as the situation where predators consume prey disproportionately to the relative abundance of different prey types.
relative rates of effective search for the different prey types (Mace 1983). As sculpins grow, their rates of effective search for fish probably increase relative to that for invertebrate prey. Then the effect of increases in the abundance of alternate prey on predation on fish will be greater for small fishes than for larger ones. More precisely, the proportional reduction in principal prey eaten, as alternate prey availability increases, will diminish as the sculpin grows. An example is given in Table 1. It is apparent from this example that the effect is small relative to the direct influence of elevated rates of effective search on the consumption of principal prey at a given prey density.

2.2.5 **Prey Size**

Larger prey can generally swim more rapidly, and are thus better able to escape attack. This is unlikely to be a factor for an ambush predator, however, since the predator relies on the prey being near enough that it has little time to react. Also, larger prey will be more difficult to manipulate. This consideration is probably irrelevant for sculpin predation since their gape size is extremely large (Hyatt 1979) and they are commonly observed to consume prey much larger than salmon fry. Finally, in natural situations, larger prey are usually older and thus more likely to be experienced in predator avoidance. The role of experience in
Table 1. The effect of increases in \( a(1) \), the rate of effective search for principal prey, on the reduction in \( N\alpha(1) \), the number of attacks per predator on principal prey, as alternate prey abundance increases. Calculations are based on the two species form of the disc equation:

\[
N\alpha(1) = \frac{a(1) N\alpha(1) T_T}{(1 + a(2) h(2) N\alpha(2) + a(1) h(1) N\alpha(1))}
\]

1) \( a(1)=1.0, h(1)=0.05, a(2)=1.0, h(2)=0.01, T_T=1.0 \)

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<th>( N\alpha(1) )</th>
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2) \( a(1)=5.0 \), all other parameters unchanged

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nature may be a major one (Dill 1974, Patten 1977); however it is not expected to be significant in the present study since naive prey were used in nearly all experiments.

On the other hand, both the increased size of the prey and their greater swimming ability may increase their rates of encounter with predators. The former will only be a significant factor if the reactive field of the predator is limited by its visual acuity; this would seem unlikely for a predator such as a sculpin.

Therefore, there are no compelling reasons to predict a pronounced prey size effect. It is possible that predation rates might increase (due to greater encounter rates) or decrease (due to enhanced prey avoidance capabilities) as prey size increases. However, I would doubt that either of these effects are great, since only a small size range is involved and the total time of exposure of fry to sculpins is short.

2.2.6 Turbidity

Prickly sculpins and chum fry coexist in a wide variety of habitats. The small coastal streams where sculpins often dominate the biomass of resident species (e.g., Mason and Machidori 1976) normally have very clear water except during high flow events. On the other hand, large estuaries such as that of the Fraser River often have very turbid waters (10-
60 formazin turbidity units in the Fraser during the spring).

The influence of turbidity on the functional response depends entirely on the attack tactics of the predator. If the distance at which a predator attacks its prey is determined by the maximum distance at which the prey can be sighted, then increasing turbidity will have a substantial impact on the predator's reactive field. In a study of planktivorous predation, Vinyard and O'Brien (1976) showed that turbidity levels had a major effect on bluegill (Lepomis gibbosus) reactive distances to Daphnia pulex and that this effect was greatest at high light levels and for large prey. Their data would suggest that reactive distances tended to decrease approximately linearly with increasing turbidity, at a given level of light intensity. If, on the other hand reactive distances are normally very small, or nonvisual cues are used to detect prey, variations in turbidity will be of minimal significance. There is no evidence in the literature that sculpins use non-visual cues, but since I expect them to be ambush predators, I would predict that turbidity would not be important.

2.2.7 Temperature

Changes in temperature may affect the functional response in two ways, first by affecting swimming speeds of the prey and second by altering the metabolic
requirements and digestion rates of the predator. The former will influence the predator's rate of effective search while the latter relates to the size of the maximum daily ration. Given the relatively small range of temperatures normally observed in coastal streams and estuaries during the spring (5-12°C), however, I do not this factor to play a major role in the sculpin-chum fry interaction.

2.3 Summary of Research Expectations and Experimental Approach

Based on the preceeding discussion, I have chosen the following set of seven predictions, or expectations, to form the basis of my experimental work.

1. Prickly sculpins will have a Type III functional response to the density of chum salmon fry, especially when alternate prey are present.

2. Rates of effective search for chum fry will fall in the range of 1.0-8.0 m²/hr, whether sculpins are ambush predators or stalk their prey.

3. Large (150 mm total length) sculpins will have a maximum ration of 2.5-4.0 chum fry per feeding.

4. Encounters of chum fry with sculpins are essentially random (Poisson) processes, such that a stochastic model based on a random search process
will describe the distribution of attacks by individual predators.

5. Observed rates of effective search will be inversely related to alternate prey abundance, but maximum ration will be unaffected by this factor.

6. Search rates and maximum rations will both increase with increasing predator size.

7. Sculpins will not prey selectively on certain sizes of prey.

My principal interest in this study concerned the first five of these predictions, which comprise features of the basic functional response. Accordingly, the focus of my experimental work was the field measurement of the functional response of prickly sculpins to chum fry. By collecting functional response data in the field, and fitting these data to both a deterministic and stochastic model, it would be possible to compare each of these five predictions to actual observations. To assist in my evaluation of the second prediction, I conducted a small series of laboratory observations of sculpin reactive distances and capture success.

To evaluate my predictions concerning the influence of alternate prey (#5), I monitored changes in the abundance of alternate prey during my experiments to measure the functional response, and examined whether these changes were
associated with changes in predation rates on chum fry. Later, I conducted an experiment in which alternate prey abundance was deliberately manipulated and the effect on sculpin feeding observed. Finally, I measured the functional response at two locations: one (Fraser estuary) with alternate prey present, and a second (Rosewall Creek) with alternate prey excluded. I examined the sixth prediction by measuring functional responses for three different sizes of predator, and the seventh by comparing the size of prey consumed to the sizes available to the predator.

My research was not directed towards investigating any of the other questions raised earlier in this Chapter (i.e., numerical responses, interference competition), since my expectation was that these factors would not exert a strong influence on the particular predator-prey interaction I chose to study. I did monitor temperature and turbidity during some of my functional response experiments, however, and the two sites chosen for my experiments offered a striking contrast in the latter of these parameters. Therefore my experimental results are able to shed some light on the issue of the influence of these two abiotic factors.

In addition to conducting experiments to evaluate the seven predictions stated above, I was interested in drawing inferences from my results regarding the population level consequences to chum salmon of prickly sculpin predation. To this end I conducted a predator sampling program, aimed at
characterizing the distribution, abundance and feeding habits of sculpins in their natural environment. Finally, I also examined sculpin gut evacuation rates and digestive pauses in the laboratory. Such information is necessary if one wants to know how often sculpins can feed to satiation in their natural environment, a fact that is critical in determining the overall impacts of sculpin predation on their prey.
III EXPERIMENTAL METHODS

3.1 Study Sites

3.1.1 Fraser Estuary

In 1979 and 1980, my field studies were conducted in the tidal marshes of the Fraser estuary. These marshes are estimated to cover an area of 3563 hectares (Anon 1978) and are now known to provide rearing habitat for millions of juvenile chum and chinook salmon (Levy et al. 1979, Levy and Northcote 1981). Within this area, Woodward Island has been found to support the greatest concentration of salmon fry during spring (Levy and Northcote 1981). A small tidal channel on Woodward Island (Figure 3) provided the study site for the functional response experiments.

3.1.2 Rosewall Creek

In 1981, I carried out additional field studies at Rosewall Creek, a small creek located on the east coast of Vancouver Island, that drains into the southern end of Baynes Sound, about 35 km south of Courtenay, B.C. Rosewall Creek, in marked contrast to the Fraser, supports only small natural stocks of chum and coho (Oncorhynchus kisutch) salmon.

A small side channel, originating in freshwater and
Figure 3. Location of the Fraser estuary study site.
having a distinct mouth in the estuary, provided the location for the field studies (Figure 4). The channel was approximately 0.5 km long and had an average width of about 4 m, except near its mouth. Within the freshwater portion of the channel a small subsection had sufficiently slow currents to allow use of enclosures with a fine enough mesh to exclude alternate prey. The water was nearly always exceedingly clear, thus providing a sharp contrast to the turbid waters of the Fraser estuary. This clarity also allowed direct observation of sculpins and fry within the stream.

3.2 Functional Response Experimental Design

3.2.1 Fraser Estuary

General Approach

A fine meshed, "fish-proof" enclosure was placed in a small tidal channel such that at high tide it was full of water but contained no salmon fry or predators. Then, known numbers of prey and predators were introduced, to be recaptured when the enclosure drained on the falling tide. By varying the numbers of prey added to the enclosure, it was possible to assess the predator's functional response.

Enclosure Design

The enclosure was located in a small tributary channel
Figure 4. Location of the Rosewall Creek study site. The stippled area represents the intertidal zone. All experiments and sculpin trapping were carried out in the experimental side channel.
near the mouth of one of the main channels draining Woodward Island ("Wl" or "Stump TC" of Levy and Northcote 1981). Its walls were made of 6.35 mm mesh seine netting with a float line at the top and a lead line at the bottom. The lead line was attached to a wooden base frame which was in turn firmly anchored into the mud substrate. The float line was secured to seven stakes which were anchored at the four corners and at the midpoints of three sides of the enclosure. This ensured that the enclosure would retain its rectangular shape despite the action of tidal currents.

To facilitate prey recapture at the termination of an experiment, it was necessary to enhance the drainage capabilities of the enclosure. A drainage ditch was dug from the downstream end of the enclosure down to a point near the mouth of the tidal channel (Figure 5). Water drained out of the enclosure through a 6.35 mm mesh net at the entrance to the drainage ditch. Fish remaining in the enclosure at the end of an experiment were easily captured in this net.

The enclosure included 30 m$^2$ of tidal channel within its approximately rectangular perimeter. At the time of termination of each experiment only 7 m$^2$ of this area was submerged.

Source and Treatment of Prey

Both chum and chinook fry were used as prey in the 1979 experiments. Out of a total of 34 experiments, chum fry
Figure 5. The experimental enclosure in the Fraser estuary, showing the system used to facilitate complete drainage and thus recapture of prey. Arrows indicate the direction of water flow.
were employed in 25 while chinook were used in the remaining nine. All prey were collected in the estuary, using a seining procedure described in Levy et al. (1979). They were held in floating pens at a dock on Westham Island, approximately 2 minutes by boat from the enclosure. Fry were never held for more than 10 days before being used in an experiment. Approximately 36 hours prior to an experiment, the desired number of prey were counted into a separate holding pen and held there until the start of the experiment. No attempt was made to restrict prey to a specified size range.

In 1980, conditions were more carefully controlled. Chum fry were used in all experiments and were obtained at the start of the field season from a Salmonid Enhancement Program facility at Inches Creek, a tributary of the Fraser River. The same holding facilities were used as for the 1979 study. In an effort to hold prey size constant throughout the field season, the fry were fed only once every two days. The pre-experimental procedure was the same as in 1979 except that the fry were counted out 16-24 hours prior to an experiment.

Source and Treatment of Predators

Prickly sculpins were collected from the estuary using unbaited wire minnow traps with enlarged openings. They were held in floating pens at the Westham Island dock. Fish being held for future experiments were offered non-live food, although subsequent observations suggested that it is
unlikely this food was eaten. In 1980 no sculpins were held for more than 10 days prior to being used in an experiment. 36 hours prior to an experiment the desired number of sculpins were counted into a mesh bag and deliberately starved until the start of the experiment. Sculpins sacrificed after 36 hours of starvation invariably had empty stomachs.

**Experimental Procedure**

Experiments were performed during falling tides, on days for which the tidal fall was sufficient to entirely drain the enclosure. All experiments were terminated when the water level in the enclosure dropped to a depth of 50 cm at the deepest point. This termination point was selected to minimize the probability of predators and prey concentrating in a small area.

The time of initiation of the experiment was calculated by first estimating from tide tables the time at which termination would occur. Experiments were started 4.5 hours before this time. Since this estimate was not exact the actual lengths of experiments varied between four and five hours. After releasing predators and prey, the enclosure was left undisturbed until shortly before the time of termination.

Experiments were terminated by using an electrofishing device to stun and recapture the predators. The sculpins were then sacrificed and placed in a 10% formalin solution
for at least 48 hours, after which they were transferred to a 40% isopropyl alcohol solution. A dissecting scalpel was used to make an incision into the abdomen of all predators before fixation to minimize the possibility of any post-mortem digestion of food.

Prey were recaptured later, when the only water remaining in the enclosure was in the drainage channel. All prey were preserved in 10% formalin (24 hours minimum) followed by 40% isopropyl alcohol.

In 1980, information was gathered regularly on three features of the enclosure environment which were discussed in Chapter 2. At the termination of each experiment, surface water temperature was measured to the nearest 0.5°C and a water sample (also at the surface) was taken for turbidity analysis. Also, regular samples of alternate prey (epibenthic macroinvertebrates) were taken by placing a plastic screen (1.5 mm diameter mesh size) on top of the fry collecting screen before the start of an experiment. This screen was then removed and its contents preserved in 10% formalin after the enclosure had drained completely at the end of an experiment. Alternate prey samples were taken during every third or fourth experiment, throughout the 1980 field season.

Treatment Schedule

Table 2 describes the experimental design for the 1979
Table 2. Experimental design for the Fraser estuary functional response experiments. Each column in this table corresponds to a distinct period of extreme tidal variation (see text). Rows correspond to days within each of these periods. The entries in each row/column combination are in the format of prey numbers : predator numbers added to the enclosure.

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<table>
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<tr>
<td>8</td>
<td>20:2 NE NE NE 160:5</td>
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NE - no experiments were conducted on these dates.
* - these experiments are not included in the analysis (Chapter 4) due to logistical problems on these dates.
and 1980 experiments. Predator densities were determined by using the maximum number that would be expected in total to consume no more than 15% of the prey available. These estimates were obviously more accurate in 1980 than in 1979, since the previous year’s data could be used to predict exploitation rates. Experiments could only be conducted during alternate weeks, since tidal variations were sufficiently extreme to drain the enclosure during half of each 28 day lunar cycle. At least one replicate of each prey density treatment was included in each one week series of experiments.

Laboratory Analyses

All recaptured prey were counted when they were transferred from formalin to alcohol. Also at this time standard lengths (in 1979) to the nearest 0.1 mm and blotted wet weights (both years) to the nearest 0.01 g were measured from the entire recapture sample or a subsample of 20 fry, whichever was less. Sculpin total lengths were measured to the nearest 1 mm and, in 1979, wet weights were recorded. Their stomachs were dissected out by cutting the esophagus and small intestine. Only the stomach was examined for food. Stomach contents were spread out in a petri dish for examination. Most contents could be easily identified with the naked eye; however a binocular microscope was occasionally used for smaller items. Major prey items were identified to genus or species, while less common items were
identified only to order or class. All items were counted and divided into two categories - fry and other prey - for weighing (wet weights). In 1979 standard lengths were recorded for all consumed fry which were sufficiently fresh to make this measurement possible.

In 1980, water samples were analysed for turbidity by a photometric method. All samples were vigorously agitated previous to analysis to ensure complete resuspension of all particulate matter. Turbidity was expressed in terms of formazin turbidity units (FTU).

Alternate prey samples were first sorted to separate whole organisms from detrital material. All organisms were identified using the same criteria for discrimination as for the predator stomach contents. Each group was counted and blotted wet weights were taken. Finally the organisms were placed in small aluminum foil dishes and left overnight in a drying oven at 60°C. Dry weights were then recorded using an electrobalance.

3.2.2 Rosewall Creek

Enclosure Design

Three identical enclosures were used in the Rosewall Creek experiments. They were smaller than the one used in the Fraser estuary, measuring 3 m x 3 m square. A fine meshed (1.5 mm diameter) plastic screening material was used
in their construction and, in addition to the four walls, a floor was sewn into each. The small mesh size and the presence of a floor excluded all organisms from the enclosures which might have supplied a natural source of alternate prey for the sculpins. Since these enclosures were not placed in tidal waters they did not drain at the end of each experiment. Therefore it was necessary to be able to remove them to facilitate recapture of prey (Figure 6).

**Prey and Predator Sources and Treatment**

Chum salmon fry were used as prey in all experiments at Rosewall Creek. They were obtained from an experimental fish hatchery on Rosewall Creek, where they were held in large, circular holding tanks and fed ad libitum. By rearing eggs from early and late spawning adults at a variety of water temperatures, a supply of "swim-up" stage fry was made available throughout the spring. All fry used in experiments ranged from 0.4-0.7 g live wet weight.

Prior to an experiment, the desired number of fry for each enclosure was counted into a 25L pail and transported to small (20L) floating holding pens inside each enclosure. For overnight experiments the fry were released into the enclosures one hour after having been placed in the holding pens. For the shorter experiments (see below) fry were held for approximately 12 hours prior to release.

Most of the sculpins used in experiments were collected
Figure 6. A depiction of the design used to hold the Rosewall Creek enclosures in place in the creek, yet facilitate easy removal. The plastic loop could be removed from the anchored stake, thereby allowing detachment of the cylindrical stake and the enclosure.
from Rosewall Creek; however large individuals (>140 mm total length) were very scarce in the Rosewall system. Therefore a supply of large sculpins was obtained from the estuary of the Little Qualicum River, a much larger system located 26 km south of Rosewall Creek.

All predators were held in 300L tanks at the hatchery. They were fed hatchery fry when they were not being prepared for experiments. No feeding was allowed for five days prior to an experiment.

On the day of an experiment, the desired number of sculpins for each enclosure was counted into a 25L pail with screen windows on the side. These pails were then placed in one of the 300L predator holding tanks. One half hour before the start of an overnight experiment or 12 hours before a shorter experiment the sculpins were transported to the enclosures and released into them.

**Experimental Procedures**

Experiments were initiated by releasing the fry from the holding pens into the enclosure. Two experiment lengths were used. Most experiments lasted 15 hours extending from 1700 to 0800 the following day. Exploitation problems prevented consideration of low prey densities for such long experiments. Thus, a series of shorter experiments lasting only 3 hours (0500-0800) were performed. In the analyses presented in Chapter 4, the results of the 15 and 3 hour
experiments were lumped by assuming that prey densities in the 3 hour experiment were one-fifth as great as actually used, instead of the experiment being one-fifth as long. This assumption is justifiable provided the prey densities in the 3 hour experiment were sufficiently low that the functional response was not approaching its asymptote (i.e., handling time is not important).

At the end of each experiment, the predators were recaptured with a long handled dip net, measured (total length) and their stomach contents removed using a gastric lavage technique (Seaburg 1957). All stomach contents were preserved in 5% formalin. Sculpins were then returned to the holding pens at the hatchery where they were held for at least five days before being used in another experiment. All fry were recaptured, counted and then released into the creek.

Treatments

Five prey densities were used in the functional response experiments, ranging from 20 to 320 prey. Predator densities were selected using the same criterion used in the Fraser estuary experiments - maximum exploitation should be no more than 15%.

Three parallel series of functional response experiments were performed on three different predator size classes (80-100 mm, 110-130 mm, >140 mm, total length).
Prey densities were the same for all three sizes but predator densities varied since exploitation effects were much greater when larger sculpins were used. Table 3 describes the experimental design for these experiments.

3.3 Alternate Prey Experiment

In addition to measuring the functional response in the absence of alternate prey, a series of experiments was performed at Rosewall Creek to determine the effect of varying the availability of alternate prey on the rate of predation at a chosen fry density.

Amphipods (Eogammarus sp. and Corophium sp.) and isopods (Gnorimosphaeroma sp.) were collected from the estuary of Rosewall Creek at low tide, weighed and held live in 25L containers. Four alternate prey treatments were used in the experiments (Table 4). Due to the substantial difference in size between chum fry and alternate prey, comparisons of prey availability were made on a biomass rather than an abundance basis.

The experimental procedure was similar to that employed in the functional response experiments, with the following exceptions. Experiments lasted only six hours, beginning at 0230. All prey were added to the enclosure on the afternoon preceding an experiment; at about the same time, sculpins were placed in the small, floating pens normally used for
Table 3. Experimental design for the Rosewall Creek functional response experiments. Each table entry is in the format prey numbers added: predator numbers added: predator size (L-large: >140mm; M-medium: 110-130mm; S-small: 80-100mm). See Table 3 for explanation of other symbols (*, NE).

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<tr>
<td>4/7</td>
<td>40:3:M</td>
<td>20:4:S</td>
<td>80:3:M</td>
</tr>
<tr>
<td>4/15</td>
<td>320:4:M</td>
<td>80:4:S</td>
<td>40:3:M</td>
</tr>
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<td>4/16</td>
<td>160:4:M</td>
<td>40:4:S</td>
<td>20:3:M</td>
</tr>
<tr>
<td>4/28</td>
<td>320:4:L</td>
<td>20:2:L</td>
<td>80:3:L</td>
</tr>
<tr>
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</tr>
<tr>
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<td>80:3:M</td>
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<td>40:2:L</td>
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<td>20:3:M</td>
<td>20:3:M</td>
</tr>
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<td>5/31</td>
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<td>80:3:M</td>
</tr>
<tr>
<td>6/1</td>
<td>40:3:M</td>
<td>40:3:M</td>
<td>40:3:M</td>
</tr>
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Table 4. Experimental design for the Rosewall Creek alternative prey experiments.

<table>
<thead>
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<th>Parameter</th>
<th>Details</th>
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</thead>
<tbody>
<tr>
<td>Dates of experiments</td>
<td>May 20-21, 25-26</td>
</tr>
<tr>
<td>Number of replicates for each treatment</td>
<td>3</td>
</tr>
<tr>
<td>Number of predators per experiment</td>
<td>5</td>
</tr>
<tr>
<td>Predator size</td>
<td>110-130 mm</td>
</tr>
<tr>
<td>Alternate prey* additions (g wet weight)</td>
<td></td>
</tr>
<tr>
<td>control</td>
<td>0</td>
</tr>
<tr>
<td>low</td>
<td>15</td>
</tr>
<tr>
<td>medium</td>
<td>45</td>
</tr>
<tr>
<td>high</td>
<td>135</td>
</tr>
<tr>
<td>Chum fry additions:</td>
<td></td>
</tr>
<tr>
<td>number</td>
<td>80</td>
</tr>
<tr>
<td>wet weight (g)</td>
<td>45</td>
</tr>
</tbody>
</table>

* The alternate prey consisted of a mixture of *Eogammarus confervicolus*, *Gnorimosphaeroma oregonensis* and *Corophium* sp.
chum fry. Experiments were initiated by releasing the sculpins into the enclosures. After the end of an experiment preserved stomach contents were returned to the lab where they were sorted, counted and weighed (wet weights).

3.4 Field Observations

3.4.1 Fraser Estuary

Observations by D. Levy (personal communication) and others suggested that prickly sculpins were one of the most abundant potential predators of salmon fry during the latter's period of estuarine residence. As part of the 1980 field studies, I carried out a sculpin trapping study to assess their distribution and abundance in the estuary throughout this period. Sculpins were routinely collected from March through June in unbaited wire minnow traps from 14 locations in three different habitat areas: slough areas, marsh edges and tidal channels (Figure 7). Traps were emptied every second day with the numbers caught and total length of each fish in the catch being recorded for each trapping location. Most captured sculpins over 80 mm total length were tagged with individually coded metal fingerling tags, attached at the base of their dorsal fin, and held for 2-8 days before being released at their site of capture. A total of 942 sculpins were tagged during the 1980 field season, 183 in slough areas, 700 at tidal marsh edges and 59 in tidal channels. Sculpins over 80 mm that were not tagged
Figure 7. Locations of the sculpin trapping sites in the Woodward Island area. The two tidal channels studied were named "W1" and "W2" by Levy and Northcote (1981). Trap sites are identified as "t" - tidal channel; "m" - marsh edge; or "s" - slough sites.
were either held for use in the functional response experiments or sacrificed for analysis of stomach contents. Sculpins were also collected for stomach contents analysis on 1979; a total of 105 sculpin stomachs were examined over the two years. Laboratory procedures were identical to those used in the functional response experiments.

3.4.2 Rosewall Creek

Prickly sculpins were routinely sampled in the side channel of Rosewall Creek used for the functional response experiments to provide information on sculpin distribution, abundance and feeding habits. Two sections of the channel were sampled intensively, one entirely in freshwater and the other in the estuary (Figure 8). Within each of these sections two habitats were sampled: pool areas (cover generally close by) and open water areas (little cover).

All sculpins were collected using unbaited wire minnow traps, which were emptied daily during a sampling period. For most of the spring a sampling period lasted four days, followed by four days without sampling. The last three samples only lasted for three days, however, with a longer non-sampling period between each.

Total lengths were measured for all captured sculpins. All fish > 60 mm were examined for the presence of marks and, if unmarked, had half the caudal fin removed (freshwa-
Figure 8. Detail of the Rosewall Creek experimental channel, showing the locations (x) of the sculpin trapping sites. Also shown is the division of the channel into three reaches for the model discussed in Chapter 6.
ter - lower half of fin; estuary - upper half). To test for mortality resulting directly from marking, 20 sculpins were marked (10 upper caudal, 10 lower) and held in tanks at the hatchery. These fish were routinely checked for disease or mortality throughout the period of the mark-recapture study.

All fish > 80 mm had their stomachs flushed using the same technique as in the functional response experiments. Stomach contents were evaluated qualitatively. This evaluation was recorded in the form of a subjective index of stomach fullness ranging from 0 (empty) to 3 (very full). As well, major food types were recorded and all contents which included suspected salmon fry remains were preserved for further analysis.

Diurnal changes in the distribution of sculpins were also observed by checking traps at various times during the diurnal cycle. Two sampling programs were employed. The first program involved checking a series of traps each day for 8 consecutive days at dusk and shortly after dawn. In the second, traps were checked before dusk, after dusk, before dawn and after dawn on 4 occasions.

3.5 Laboratory Studies

3.5.1 Design of the Observational Apparatus

Two identical rectangular aquaria (61 cm x 30.5 cm) were used to measure sculpin reactive distances and capture
success when offered chum fry as prey (Figure 9). The sides and rear walls of the aquaria were opaque and a light grey color, while the front wall was transparent. They were placed on separate 1.3 m tall stands in a wet lab at the Rosewall Creek hatchery.

Surrounding the front and sides of both tanks at a distance of approximately 1 m was a floor-to-ceiling blind made from 6 mil black polythene. Directly opposite the front of each tank was a small (2 cm x 6 cm) rectangular hole through which observers could monitor activities in the aquaria without disturbing the fish under observation.

Suspended above each aquarium at an angle of approximately 45° was a rectangular mirror (45.7 cm x 30.5 cm). The mirror angled upwards towards the front of the aquarium with its lower edge resting on the rear wall. The bottom of each aquarium was marked out into a grid of 2 cm squares. By observing sculpin attacks in the mirror with the gridded tank floor as a reference, measurements of reactive distance could be made. The blind was sufficiently far away from each aquarium, and the observation hole was sufficiently large, that surveillance of both the mirror and the front windows at the same time was possible.
Figure 9. Apparatus used for laboratory observations of sculpin feeding.
3.5.2 Procedures

Reactive Distances

Thirty minutes before the beginning of each observation period, a single sculpin was placed in each aquarium. An observation period began with the addition of an individual chum fry (0.4-0.6 g wet weight) in a small quantity of water, poured into the water supply inlet pipe (Figure 9). As soon as a fry was eaten it was replaced by another. More often, individual fry would exhibit behaviour which rendered it very unlikely that predator-prey encounters would occur (e.g., motionless, swimming at or near the surface only). When this occurred more fry were added, usually one at a time, until encounters began to occur.

All encounters (defined as sculpin-fry separations of less than 10 cm), attacks and captures and their respective distances were tape recorded for later analysis. Additional general observations about the behaviour of the sculpins or any fry were also recorded.

Observations were continued for 30 minutes or until it became apparent that the sculpin was no longer interested in taking fry. In virtually all instances the latter criterion was met before the former.

Sculpins representing all three size classes used in the Rosewall functional response experiments were analysed in this way. The objective was to make as many observations...
as possible of successful attacks for each size class, up to a maximum of twenty.

Hunger/digestion

To measure the time elapsed before a satiated sculpin returns to a state of hunger sufficient to prompt further consumption, 20 chum fry and one hungry sculpin were placed in an aquarium for one hour. After this time the sculpin was removed and placed in a holding tank without food. The remaining fry were counted, and the number eaten recorded. Every 24 hours for five days following this feeding the sculpin was returned to an aquarium with 20 fry for one hour to see whether it would resume feeding. Eight large and four small sculpins were employed in these trials. As well, five medium sculpins were similarly treated but tested for resumed hunger at less regular intervals.

Observations were also made on rates of gastric evacuation of chum fry by sculpins under conditions of a single feeding followed by starvation. Sixteen medium sculpins were used in this analysis. Water temperatures varied between 7 and 9°C. Having consumed at least one and no more than three fry, the sculpins were held without food for varying lengths of time (2 each at 2, 4, 8, 16, 24, 36 and 48 hours). At the end of the designated time period, each sculpin had its stomach flushed using gastric lavage. The contents were preserved in 5% formalin for further analysis.
IV THE PRICKLY SCULPIN FUNCTIONAL RESPONSE

4.1 Parameter Estimation Methods

4.1.1 Fujii Model

To estimate the parameters of the functional response, as discussed in Chapter 2, I have selected the Fujii model (equation (5)) (Fujii et al. 1978), as the most appropriate representative of the group of models that have been derived from the disc equation. The Fujii model offers the advantage of being capable of describing all four functional response types. Since this equation (and all other models which extend the disc equation) is non-linear in its parameters, I have used numerical methods for parameter estimation.

I performed the analysis on an Amdahl V8 computer by minimizing a least squares objective function using the "FLETCH" algorithm (Fletcher 1970), a quasi-Newtonian method for function minimization (Patterson 1978). For a normally distributed dependent variable with homogeneous variances, least squares estimates correspond to maximum likelihood estimates for a given parameter. In this case the dependent variable is far from normal, being skewed to the right at low prey densities.
To evaluate the bias introduced by this departure from normality, I conducted a simple simulation experiment. By assuming a Poisson distribution of successful attacks (supported by my data - see Chapter 6, Table 12), and specifying the parameters \( (A_{\text{max}}, g, c) \) of the Fujii model, I was able to use Monte Carlo methods to generate simulated functional response data. I then obtained parameter estimates for the simulated data and compared these estimates to the true parameter values.

Results are presented in Figure 10 for two parameter combinations. Each point represents the mean estimate of a parameter from ten simulated datasets. It is evident from these figures that the bias is minor for estimates of \( A_{\text{max}} \), and is only large for \( g \) and \( c \) when sample sizes are small. Since my sample sizes typically ranged between 10 and 20 observations at each prey density, this bias may influence my results.

The primary reason for the biases in \( g \) and \( c \) stems from the fact that these two parameter estimates tend to be highly correlated. Anomalously large estimates of \( g \) from the simulated datasets were invariably associated with comparably large estimates of \( c \). Overestimates of \( g \) will be reflected in underestimates of rates of effective search, if \( A_{\text{max}} \) is unbiased, since \( g = 1/(a'\cdot h) \). However, since the rate of effective search at a given prey density is given by
Figure 10. Estimated bias in the parameters of the Fujii model assuming that attacks are distributed according to a Poisson distribution. Means ± ranges for parameter estimates are shown for two sets of simulations, as a function of the number of observations at each prey density. The true values for the parameters (indicated by the dashed lines) were set at: $A_{\text{max}}=2.5$; $g=3.0$; $c=0.7$ (A); and $A_{\text{max}}=1.2$; $g=3.2$; $c=0.0$ (B).
underestimates of $a'$ will tend to be counteracted by overestimates of $c$. Thus the bias in the estimate of $a$ will tend to decrease as prey density increases.

In the Fraser estuary, tidal fluctuations in water level resulted in changes in prey density during the course of each experiment. To obtain accurate parameter estimates, the estimation procedure had to account for these changes. To accomplish this, I developed a simple model to describe the changes in prey density during the course of an experiment as a consequence of changes in the wetted area of the enclosure.

Since all experiments were of approximately the same length, and occurred during a similar period of the tidal cycle, a single model could be used to describe changes in wetted area. The enclosure was completely wetted for the first three hours, after which the wetted area decreased until the termination of the experiment. The wetted area began to decrease at intermediate tidal heights; at this time the water level drop was almost linear with time. This fact, combined with the even grade of the enclosure floor, resulted in an approximately linear decrease in wetted area for the final 1.5 hours of each experiment. Given a total wetted area of $30 \, \text{m}^2$ at the start of an experiment, and $7 \, \text{m}^2$ at the conclusion, the following simple model describes this
pattern:

\[ A(t) = 30. \quad t < 3 \text{hr} \quad (19) \]

\[ A(t) = 30. - 15.3 \cdot (t-3.) \quad 3 \text{hr} < t < 4.5 \text{hr} \]

where \( t = \) hours from the start of the experiment; and

\[ A(t) = \text{area (m}^2\text{)} \text{ at time } t.\]

I thus incorporated this model into the Fujii equation, and then integrated over changing prey densities to give the final prediction of attacks over the experimental period:

\[
N_a = \int_{t=0}^{t=T} \frac{A_{\max} \cdot N_0 / A(t)}{g \cdot \exp(-c \cdot N_0 / A(t)) + N_0 / A(t)} \, dt, \quad T = 4.5 \text{hr} \quad (20)
\]

To solve this integral I incorporated a numerical integration procedure into the overall parameter estimation procedure. A simple simulation experiment indicated that an integration time step of 0.1 hours was sufficient to give accurate estimates of the rates of attack. For comparison, I also analysed the Fraser estuary experiments assuming constant areas of 30 m\(^2\) and 7 m\(^2\).

4.1.2 **Stochastic Model**

The stochastic model predicts a multinomial distribution of attacks; therefore the likelihood function can be
written as*:

\[ L(\tilde{a},m) = p_{0,m}^{n_{0,m}} \cdot p_{1,m}^{n_{1,m}} \cdots p_{k,m}^{n_{k,m}} \]  \hspace{1cm} (21)

where \( \tilde{a} \) = vector of parameters \( a_0 \ldots a_k \); 
\( m \) = experiment \((1 \ldots M)\); 
\( p_{k,m} \) = probability of state \( k \), for experiment \( m \); and 
\( n_{k,m} \) = number of observations of state \( k \) in experiment \( m \).

Following conventional practice, I chose to carry out the parameter estimation by maximizing the log-likelihood function:

\[ \log(L) = \sum_{m=1}^{M} \sum_{k} n_{i,m} \cdot \log(p_{i,m}) \]  \hspace{1cm} (22)

It was necessary to choose a finite number of possible states, \( k \), so I chose a range corresponding to those states observed in my experiments. To perform this analysis I used the same computing system and software as was used for the Fujii model analysis.

4.2 Form of the Response

In Chapter 2, I predicted that the prickly sculpin functional response would have a Type III

*Strictly speaking, a multinomial coefficient should be included in this likelihood function. The coefficient's value is independent of the model parameter values, however, so its exclusion does not affect the optimization problem.
form, especially in the presence of alternate prey. In fact, I observed Type III responses in 1979 and 1981, but not in 1980, as evidenced by the presence (absence in 1980) of an ascending limb on plots of the proportion of prey killed per predator versus prey density (Figures 11b, 12b, 13b). In 1980 the results are equivocal, with little or no difference in the proportion killed at the two lowest densities.

For the Fujii model, the value of the parameter "c" gives an indication of the form of the response. According to Fujii et al. (1978), a Type III response is obtained when \( c > 1/g \). Parameter estimates for the Fujii model (Table 5) suggest a Type III response only for 1981. When I excluded from the analysis the experimental results for the two highest densities used in 1979, however (see section 4.4 below for a discussion of this treatment of the data), a strongly sigmoid functional response was also obtained for this year (Figure 11a, curve C).

The stochastic model parameter estimates suggest a Type III response for all three years (Table 6). In each year, the \( a_k \) parameters tend to increase as the predator's state changes from an empty stomach \((k=0)\) to an intermediate state of fullness \((k=2,3)\). This implies that the rate of effective search increases after the predator has successfully encountered prey, a behaviour which gives rise to a Type III response. It should be noted, however, that the increases in \( a_k \) with \( k \) are far from statistically significant, as
Figure 11. Functional response results for 1979. Upper panel shows mean (±1 standard error) number of attacks at each prey density; lower panel shows mean (±1 standard error) predation rate at each prey density. Also shown on the upper panel are the fitted functional response curves from the parameter estimates in Tables 5 and 6: (a) Fujii model; (b) stochastic model; (c) Fujii model excluding two highest prey densities. Sample sizes at each prey density are shown on the lower panel.
Figure 12. Functional response results for 1980. Upper panel shows mean (±1 standard error) number of attacks at each prey density; lower panel shows mean (±1 standard error) predation rate at each prey density. Also shown on the upper panel are the fitted functional response curves from the parameter estimates in Tables 5 and 6: (a) Fujii model; (b) stochastic model. Sample sizes at each prey density are shown on the lower panel.
Figure 13. Functional response results for 1981. Upper panel shows mean (±1 standard error) number of attacks at each prey density; lower panel shows mean (±1 standard error) predation rate at each prey density. Also shown on the upper panel are the fitted functional response curves from the parameter estimates in Tables 5 and 6: (a) Fujii model; (b) stochastic model; (c) stochastic model fit using least squares method. Note that the highest prey density treatment was not included in the data used to obtain parameter estimates. Sample sizes at each prey density are shown on the lower panel.
Table 5. Parameter estimates for the Fujii model. Estimated standard errors$^a$ in parentheses. The parameter $a'$ is calculated from:

$$a' = 1 / (g \cdot h)$$

where $h = T_t / A_{\text{max}}$; and $T_t$ is the experiment length.

<table>
<thead>
<tr>
<th>Field season</th>
<th>Search area assumed</th>
<th>$A_{\text{max}}$ (# prey per experiment)</th>
<th>$g$</th>
<th>$c$</th>
<th>$a'$ (m$^2$/hr)</th>
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</thead>
<tbody>
<tr>
<td>1979</td>
<td>30 m$^2$</td>
<td>8.71(1.70)</td>
<td>9.62(2.33)</td>
<td>0.00</td>
<td>0.20</td>
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<tr>
<td></td>
<td>7 m$^2$</td>
<td>8.71(1.70)</td>
<td>41.24(9.88)</td>
<td>0.02</td>
<td>0.05</td>
</tr>
<tr>
<td></td>
<td>dynamic$^b$</td>
<td>1.99 (-)</td>
<td>12.52(-)</td>
<td>0.00</td>
<td>0.16</td>
</tr>
<tr>
<td>1980</td>
<td>30 m$^2$</td>
<td>4.23(8.46)</td>
<td>7.44(15.4)</td>
<td>0.26</td>
<td>0.13</td>
</tr>
<tr>
<td></td>
<td>7 m$^2$</td>
<td>4.23(8.46)</td>
<td>31.88(66.1)</td>
<td>0.06</td>
<td>0.03</td>
</tr>
<tr>
<td></td>
<td>dynamic$^b$</td>
<td>1.01(0.66)</td>
<td>10.46(6.77)</td>
<td>0.08</td>
<td>0.10</td>
</tr>
<tr>
<td>1981</td>
<td>10 m$^2$</td>
<td>2.53(0.12)</td>
<td>2.71(1.03)</td>
<td>0.74</td>
<td>0.06</td>
</tr>
<tr>
<td>1979$^d$</td>
<td>30 m$^2$</td>
<td>2.34(0.14)</td>
<td>52.82(93.4)</td>
<td>4.07</td>
<td>0.01</td>
</tr>
</tbody>
</table>

Notes:

$^a$ - assumes a normal distribution for the parameter estimates

$^b$ - the variable area model produced estimates of maximum consumption per hour, rather than per experiment

$c$ - a singular Hessian matrix prevented the computation of parameter standard errors

$d$ - re-analysed without the two highest density treatments
Table 6. Parameter estimates for the stochastic model. Estimated standard errors in parentheses.

<table>
<thead>
<tr>
<th>Field season</th>
<th>1979</th>
<th>1980</th>
<th>1981</th>
</tr>
</thead>
<tbody>
<tr>
<td>Search area 30 m²</td>
<td>7 m² dynamic</td>
<td>30 m² 7 m² dynamic</td>
<td>10 m² 10 m²</td>
</tr>
<tr>
<td>aₖ (m²/hr):</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>k=0</td>
<td>.05 (.04)</td>
<td>.04b (.02)</td>
<td>.06 (.03)</td>
</tr>
<tr>
<td>k=1</td>
<td>.06 (.08)</td>
<td>.05 (.04)</td>
<td>.09 (.07)</td>
</tr>
<tr>
<td>k=2</td>
<td>.15 (.18)</td>
<td>.12 (.08)</td>
<td>.27 (.20)</td>
</tr>
<tr>
<td>k=3</td>
<td>.65 (.26)</td>
<td>.50 (.14)</td>
<td>.19 (.18)</td>
</tr>
<tr>
<td>k=4</td>
<td>.13 (.15)</td>
<td>.10 (.07)</td>
<td>.13 (.21)</td>
</tr>
<tr>
<td>k=5</td>
<td>.12 (.21)</td>
<td>.10 (.07)</td>
<td>.12 (.26)</td>
</tr>
</tbody>
</table>

Notes:

a - These estimates were not obtained by integrating $p_k(t)$ over time while letting $N_Q$ vary with area. Instead they were derived by interpolating between the 30 m² and the 7 m² estimates, assuming an "effective area searched" of 23.28 m². The "effective area searched" was derived by contrasting the dynamic and non-dynamic results from the Fujii model parameter estimation.

b - A singular Hessian matrix prevented the estimation of standard errors for these estimates.

c - Least squares estimates for the 1981 results.
indicated by the large standard errors.

Woodsworth (1982) did not observe a Type III functional response in a laboratory study of prickly sculpins feeding on sockeye salmon (O. nerka), even in the presence of alternate prey (salmon eggs). This result may be the consequence of his not considering sufficiently low prey densities to detect the sigmoid shape of the response, however. Woodsworth's minimum prey density-time of exposure combination was substantially higher than those utilized in this study. In a study of staghorn sculpins (Leptocottus armatus) feeding on chum fry, Mace (1983) observed a Type III functional response for the largest sculpins she considered, in the absence of alternate prey. While the "large" sculpins in her study were much smaller than my "large" sculpins (<100 mm versus >140 mm total length), the ration levels (as seen in her Figure 6.3) appear comparable.

4.3 Rate of Effective Search

In Chapter 2 I predicted that the rates of effective search should range from 1. to 8. m²/hr, regardless of the mode of predation (ambush or stalk) used by sculpins. For the Fujii model, the rate of effective search for prey densities approaching zero is given by a' (= 1/(g h)). If the parameter "c" is positive, the rate of effective search increases exponentially as prey density increases. When "c" is zero, the rate of effective search is constant at all
densities and the Fujii model reduces to the disc equation. For the stochastic model, the $a_k$ are estimates of the predator's rate of effective search at each state (k) of stomach fullness.

Estimates of the rates of effective search for both models and for all three years of data (Tables 5-6) are far below my predicted values, being typically at least one order of magnitude smaller. Although my experimental results appear strikingly different from expectation, it is worth noting that of all the predictions presented in Chapter 2, the second had perhaps the least empirical evidence in its support. There are thus several possible explanations for this result.

First, it is possible that the low estimates are simply a result of biases in the estimation procedure. Small sample sizes may have led to overestimates of the true value of $g$ (which determines $a'$) in the Fujii equation, due to the tendency for the data to be skewed to the right at low prey densities. In my simulation experiments, however, overestimates of $g$ were invariably associated with extremely large standard error estimates for this parameter. This was not the case for my field experimental results, except possibly for the 1979 data without the two highest densities (Table 5). In addition, the fact that the Fujii model appears to fit the data reasonably well (Figures 11-13), and that the stochastic model estimates of $a_k$ are also
low, suggests that the parameter estimates are not badly biased.

If the low estimates of rates of effective search are not an artifact of the estimation procedure, then perhaps reactive distances are much lower than I had predicted. The results of my laboratory observations, however, indicate reactive distances for large (150 mm) sculpins quite similar to expectations (Table 7). If these observations are representative of the behaviour of sculpins in the field, then this explanation seems unlikely. Similarly, capture success was observed to be only slightly less than expected, at least for large sculpins.

The third component directly involved in the computation of the expected search rates was the movement rate of the prey. The search rate estimates may be much lower than expected because average rates of movement of chum fry during the course of an experiment were actually far less than assumed in Chapter 2. It would seem quite plausible that fry movement rates, on the average, are low because they spend a considerable amount of time not moving at all. My estimates of movement rates were based on the presumption that well-fed fry would move at a rate no less than one-half that of actively foraging fish. It is difficult to think of a good reason for movement when the fry are not foraging, especially if their predators are stationary. Even if food is being sought, many fish living in flowing water systems will
Table 7. Results of laboratory observations of prey capture.

<table>
<thead>
<tr>
<th>SCULPIN SIZE CATEGORY</th>
<th>small (80-100 mm)</th>
<th>medium (110-130 mm)</th>
<th>large (&gt;140 mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>number of fish observed</td>
<td>19</td>
<td>10</td>
<td>4</td>
</tr>
<tr>
<td>number of attacks observed, all sculpins (A_0)</td>
<td>79</td>
<td>49</td>
<td>28</td>
</tr>
<tr>
<td>number of successful captures, all sculpins (A_s)</td>
<td>16</td>
<td>20</td>
<td>19</td>
</tr>
<tr>
<td>proportion captured (p_c = A_s / A_0)</td>
<td>.20</td>
<td>.41</td>
<td>.68</td>
</tr>
<tr>
<td>average reactive distance (cm) (RD)</td>
<td>3.34</td>
<td>3.52</td>
<td>3.77</td>
</tr>
<tr>
<td>effective reactive distance (cm) (RE = p_c \times RD)</td>
<td>.67</td>
<td>1.44</td>
<td>2.56</td>
</tr>
</tbody>
</table>
tend to remain more or less in one place and feed on food drifting by. This kind of behaviour was observed in Rosewall Creek during the day. Thus, there are reasons for supposing that prey movement rates were actually much lower than originally expected.

Another potential source of substantial error in the original predictions of search rates concerns the implicit assumption that the prey always remain close enough to the bottom, so that their vertical distance from the predator does not affect encounter rates. Since chum fry in the Fraser estuary appear to feed primarily on benthic organisms (Levy and Northcote 1981), and since, at Rosewall Creek, chum fry were observed to be bottom oriented, this seemed like a reasonable assumption. The motivation for a benthic feeder to stay near the bottom disappears when it becomes satiated, however. If the risk of predation is greater on the bottom than in the water column, then it would be advantageous for fry to move closer to the surface when not actively foraging. At Rosewall Creek, the fry distribution observations were made during daylight hours, while the experiments took place at night. Chum fry may move closer to the surface at night when avian predators (e.g., herons, kingfishers) do not pose a threat. Observations of the downstream migration patterns of chum and pink salmon fry by Hunter (1959) indicated a pronounced tendency for fry to remain closer to the surface than the bottom during their nocturnal movements.
How would the results be affected by a modification of my assumption about the vertical distribution of chum fry? As an example, consider the situation where fry are distributed uniformly throughout the water column, rather than being restricted to the bottom. This is easier to illustrate for Rosewall Creek, where water levels remained constant. Given a water depth of 30 cm, and assuming that fry must be within 5 cm of the bottom to be attacked by a sculpin, an individual fry would only spend one-sixth of its time within the zone of potential capture. This is effectively the same as stating that prey densities were actually one-sixth the values I assumed them to be. Thus, sculpin search rates would need to be six times the estimated values to produce the results I observed. In the Fraser estuary, the effect may have been greater, since for most of an experiment the water was deeper. Clearly, the vertical distribution of prey has an important effect on the interpretation of search rate estimates.

Finally, the rates of effective search may actually be much higher than my parameter estimates would indicate. This would be the case if my assumption from Chapter 2, that $T_t$ is equal to the length of an experiment, is actually false. It is possible that the sculpins ignored fry at certain times during the experiments. Since sculpins are prey to avian predators such as herons and mergansers, predator avoidance behaviour may reduce the time available for feeding. The benefit of avoiding a predator far outweighs the cost of not
capturing a prey item. Mace (1983) also suggested that avoidance of prickly sculpins may have strongly influenced the foraging behaviour of staghorn sculpins. She excluded large sculpins (>100 mm total length) from her experiments because they appeared completely unattentive to chum fry during daylight.

The experimental design I used in this study does not allow me to determine which of these explanations is most likely to be true. Since my experiments at both study sites included periods of daylight, \( T_c \) may have actually been less than the experiment length. It is unlikely, however, that the reduction was great enough to account for the substantial differences in expected and observed rates of effective search. Further to this, hours of daylight (measured during the 1980 experiments) did not explain a significant amount of the residual variation in successful attacks after accounting for prey density. Therefore, it would seem likely that the primary explanation for the extremely low apparent rates of search, relative to expectation, derives from errors in my assumptions about prey distribution or movement rates.

4.4 Maximum Ration

In 1979 and 1981, the functional response experiments produced a result not predicted by any conventional functional response model, and in contradiction to my
third prediction, which stated that the expected maximum ration for 150 mm sculpins would be 2.5-4.0 fry. At high prey densities (320,640 in 1979; 320 in 1981) some of the predators used in my experiments gorged themselves, consuming up to 15 fry in a single experiment. This resulted in an apparent levelling off of the functional response at intermediate densities, followed by a further rise at high prey densities. In 1980, I did not observe this behaviour, presumably since high prey density treatments were not used.

Incorporation of these high density results into the parameter estimation clearly gave a misleading picture of the functional response at low densities, as evidenced by the much improved fit of the Fujii model to my 1979 results when the two high density treatments were excluded (Figure 11). Therefore I opted to exclude the highest density in my analysis of the 1981 results as well. When these treatments were excluded, the estimates of maximum ration ($A_{\text{max}}$) are consistent with those predicted earlier.

Both Woodsworth (1982) and Mace (1983) obtained similar results in their functional response experiments. I also observed predators to gorge themselves on chum fry in both my field and laboratory observations of sculpin feeding at Rosewall Creek. As well, similar phenomena have been observed in other, quite different predator-prey systems (e.g., Clarke et al. 1967, Kruuk 1972, Sandness and McMurtry 1970, Schaller 1972).
Woodsworth suggested that the increase in consumption at high prey densities may have resulted from the sculpins switching to an alternate mode of prey detection. While such a change in behaviour might imply that the overall functional response is actually the sum of two separate responses, the question remains as to why the two responses would have different asymptotes. It would appear that at high prey densities something is stimulating the sculpins to resume feeding after reaching what might be described as satiation at lower prey densities. Further discussion of this result is left to Chapter 7, where I develop and discuss alternative models of sculpin predation on chum fry.

4.5 Fit to the Stochastic Model

As mentioned earlier, the Fujii model fits the functional response data quite well, at least when the high prey density treatments are excluded in 1979 and 1981. In contrast, the stochastic model does not fit the data well, in any of the years (Figures 11-13). Generally, the expected attack rates are too low at low densities and too high at high densities.

This result is apparently a consequence of the inability of the model to explain the high variability amongst
individual predators in their rates of attack on chum fry, even after accounting for prey density effects (Figures 14-15). Unlike the least squares method which was used to fit the Fujii model (since this model only predicts the mean number of attacks), the likelihood function for the stochastic model takes into account the complete distribution of attacks at each prey density, to obtain maximum likelihood parameter estimates. Because of the form of the likelihood function,

\[ L(\theta) = \prod_{m} \prod_{i} p_{i,m}(\theta)^{n_{i,m}}, \quad \text{or} \]

\[ \log(L(\theta)) = \sum_{m} \sum_{i} n_{i,m} \log(p_{i,m}(\theta)), \]

the occurrence of low probability events \( p_{i,m} < 0. \) can dominate its value. If any observations are made of these low probability events, \( (i.e., n_{i,m} > 0.) \) they will cause the likelihood function to become very small and thus severely penalize the parameter estimates. The estimation scheme for the stochastic model thus abhors any estimates that, although they fit the observed mean well, assign a low probability to outliers that do occur. In other words, a much greater penalty occurs if the outliers are not predicted than if the mean is missed.

In my experiments, low outliers (especially zero attacks) were common at low densities, while high outliers were often observed at high densities. Thus the stochastic
Figure 14. Observed attack distributions (shaded bars) for the 1979 (A) and 1980 (B) Fraser estuary experiments, and the expected distributions from the stochastic model (open bars).
Figure 15. Observed attack distributions (shaded bars) for the 1981 15 hour (A) and 3 hour (B) experiments at Rosewall Creek, and the expected distributions from the stochastic model (open bars).
model estimates produced expected values that were too low at low densities and too high at high densities.

If this explanation for the "poor" estimates arising from the stochastic model is correct, then using an objective function in the estimation scheme which does not include such a severe penalty for outliers should produce quite different results. The least-squares method is the obvious choice. When a least-squares objective function was used to analyse the results for 1981, the result was a much better fit to the observed mean attack rates (Figure 13). As expected, however, the parameter estimates imply far less variability in attack rates than was actually observed.

The significance of these results lies in a mechanistic interpretation of the "poor" fit of the stochastic model. Essentially, the stochastic model did not predict as much variability in attacks at a given prey density as was actually observed. This implies that a simple stochastic search model, which assumes random search and encounter processes, is not sufficient to describe the interaction between prickly sculpins and their salmon fry prey, even though it allows for search rates to be dependent on the predator's state (of hunger). Apparently, factors other than prey density and random search (and attack) are playing an important role in determining attack rates for individual fish.
5.1 Alternate Prey

5.1.1 Fraser Estuary

Three species of epibenthic crustaceans comprised the vast majority of the alternate prey, both in enclosure samples and in predator stomachs: *Neomysis mercedis*, *Gnorimosphaeroma oregonensis* and *Eogammarus confervicolus*. All three species showed a sharp increase in relative abundance early in the spring, followed by an equally rapid decline which continued through the final series of experiments (Figure 16a). To see whether this variability in alternate prey abundance influenced sculpin predation rates on fry, the results of the functional response experiments were divided into five subsets each corresponding to a specific replicate series (Figure 16b). It is apparent that when alternate prey were relatively abundant (series B,C) lower predation rates were observed, on the average, than at other times (series A,D,E).

To illustrate this phenomenon in quantitative terms I calculated the following statistic:

\[ D_{j,i} = \bar{x}_{j,i} - \bar{x}_j \]

(23)
Figure 16. Upper panel: Changes in alternate prey abundance in the enclosure during the 1980 field season. Dates of functional response replicate series are indicated by the horizontal bars. Lower panel: Functional response results for 1980 divided into results for each replicate series. Each point represents the mean number of chum fry eaten per predator in a particular replicate series. As shown in the upper panel, alphabetical order for the points implies chronological order.
where $\bar{x}_{j,i}$ = mean number fry eaten in treatment $j$, series $i$; and $\bar{x}_j$ = grand mean for treatment $j$.

$D_{j,i}$ represents the deviation of observed rates of predation in a specific series from the expected rates based on the average over the entire season. The correlation between $D_{j,i}$ and the relative abundance of alternate prey is significant ($r = -0.482$, $p<0.05$, df=18, Figure 17).

In 1979, my functional response experiments were conducted, on the average, later in the spring than in 1980 (see Table 2). If the same seasonal pattern of alternate prey availability occurred in both years, then a higher rate of effective search would be expected in 1979, since alternate prey would have been (on the average) less abundant in these experiments. Visual inspection of the results (Figures 11-12) confirms this expectation. Comparison of the parameter estimates for the two years' data is made more difficult by the fact that, in 1979, a Type III response was observed. The rate of effective search thus depends on the prey density:

$$a = a' \cdot \exp(c \cdot N_o)$$ (4)

For the two low prey density treatments (0.67 and 1.33 fry per m², assuming a constant area of 30 m²) the estimated values are 0.15 and 2.24 m²/hr in 1979, as compared to 0.13 in both cases (since $c=0$) for 1980. Thus the 1979 estimate does appear to be larger, although the difference is very small
Figure 17. The relationship between fry consumption and alternate prey availability. The open triangles represent deviations, for each treatment, of the mean fry consumption for a given replicate series from the treatment grand mean. The closed circles represent the average deviation for each replicate series, averaged over all treatments. Alternate prey relative abundances are replicate series means as shown in Figure 16a. The alphabetical code for each series is shown along the abscissa.
at the lowest prey density.

5.1.2 Rosewall Creek

When alternate prey were added to the Rosewall Creek enclosures there were significant reductions in chum fry consumption at all three levels of alternate prey abundance, as compared to the control (Table 8a). The degree of reduction varied only slightly among the three treatments (Figure 18a), suggesting that the relative availability of alternate prey (in terms of biomass) need not be very great to cause a significant shift in sculpin diet away from chum fry. Alternate prey consumption varies only slightly among the three treatments (Figure 18b) and total consumption actually declines as alternate prey availability increases (Figure 18c), although the differences are not significant (Table 8b). These observations suggest strongly that either chum fry are not a preferred prey of prickly sculpins, or that overall feeding rates were somehow inhibited by the presence of alternate prey. They are also consistent with my prediction #5 from Chapter 2 that rates of effective search will decline with increasing alternate prey abundance.

Mace (1983) also observed decreases in fry consumption in the presence of alternate prey (her Figure 6.8), but her analysis indicated a preference towards fry, relative to amphipods (*Eogammarus confervicolus*). Her estimates of preference were based on numerical comparisons of fry and
Table 8. Results of ANOVA on the 1981 alternate prey experiment. For "A", the dependent variate is the number of fry consumed per sculpin, while for "B", it is the total weight of food eaten. The four treatments were 0 (control), 15, 45, and 135 g wet weight of alternate prey added to an enclosure together with 80 chum fry (45 g wet weight) and three prickly sculpins (115-125 mm total length).

A. Chum Fry Consumption

<table>
<thead>
<tr>
<th>SOURCE</th>
<th>df</th>
<th>SS</th>
<th>MS</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total</td>
<td>59</td>
<td>42.98</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Among</td>
<td>3</td>
<td>8.45</td>
<td>2.82</td>
<td>4.57</td>
<td>&lt; .05</td>
</tr>
<tr>
<td>Within</td>
<td>56</td>
<td>34.53</td>
<td>0.62</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Duncan's New Multiple Range test indicated that the control treatment mean was significantly different from all other treatment means. The other treatment means were not significantly different from each other.

B. Total Weight of Food Eaten

<table>
<thead>
<tr>
<th>SOURCE</th>
<th>df</th>
<th>SS</th>
<th>MS</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total</td>
<td>59</td>
<td>16.42</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Among</td>
<td>3</td>
<td>0.90</td>
<td>0.30</td>
<td>1.07</td>
<td>&gt; 0.05</td>
</tr>
<tr>
<td>Within</td>
<td>56</td>
<td>15.52</td>
<td>0.28</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 18. Results of the 1981 alternate prey experiment. Means ±1 standard error are plotted.
amphipod densities, rather than biomass comparisons. In my alternate prey experiments, invertebrates were far more abundant than chum fry even at the lowest alternate prey density. Thus my results are consistent with those of Mace; the experiments indicate that predation on fry will likely be reduced in areas of high invertebrate availability, but do not necessarily demonstrate a preference for alternate prey, or chum fry. The interpretation of the results in terms of preference will depend greatly on whether numbers or biomass is the metric of availability.

The observation of similar maximum ration values for both 1979 (without high prey densities) and the 1981 results, also supports prediction #5 from Chapter 2, namely that the asymptote of the functional response to chum fry is not affected by alternate prey.

5.2 Predator Size

During 1979 I used a relatively wide range of predator sizes (120-190 mm total length) in the functional response experiments. The effect of predator size can be examined by considering the relation between an individual's size and its prey consumption in a functional response experiment, relative to the mean rate of consumption for that treatment (Figure 19). Although the results are quite variable, the correlation is significant and positive (r=.26, p<.05, df=77). Thus larger sculpins tended to consume more prey at
Figure 19. The relationship between relative predation rates and predator size, for the 1979 Fraser estuary experiments. Predation rates are corrected for treatment (i.e., prey density) effects.
a given density than their smaller conspecifics. Most notably, sculpins less than 140 mm total length consistently consumed less than the expected amount based on the mean for all predators.

The results of the functional response experiments performed on three sculpin size classes in 1981 (Figure 20, Table 9) show striking predator size effects, which support prediction #6. Not surprisingly, the most obvious difference concerns the asymptote; sculpins less than 100mm total length were rarely observed with more than one fry in their stomachs. The slope of the functional response also increases with increasing predator size, especially between the small and medium sculpins. My laboratory observations of sculpins feeding support this result (Table 7), although the differences in reactive distances between small and medium sculpins are not as great as their respective functional response curves would suggest. The differences observed in the lab are a consequence of larger sculpins having considerably greater capture success. Smaller sculpins were much more prone to stalking and chasing prey, with the result that fry soon became more wary of their presence, at least temporarily. In addition, the smallest sculpins were sometimes unable to handle fry and would lose their prey even after capturing it.

Mace (1983) observed increases in maximum ration, but decreases in rates of effective search, as predator size
Figure 20. Comparison of the functional response experimental results for the three predator size classes. The mean number of prey eaten per predator and the line of best fit to the Fujii model are both plotted for each size class. Large (>140mm) sculpins: solid line, closed circles; medium (110-130mm) sculpins: dotted line, triangles; small (80-100mm) sculpins: dashed line, open circles.
Table 9. Parameter estimates for the Fujii and stochastic models for the three sculpin size categories. Estimated standard errors (where calculable) in parentheses. For the stochastic model, dashes (-) indicate predator states that were not included in the analysis of a particular sculpin size category.

<table>
<thead>
<tr>
<th>SCULPIN SIZE CATEGORY</th>
<th>small</th>
<th>medium</th>
<th>large</th>
</tr>
</thead>
<tbody>
<tr>
<td>( A_{\text{max}} ) (number per experiment)</td>
<td>0.97 (1.95)</td>
<td>1.43 (0.12)</td>
<td>2.53 (0.12)</td>
</tr>
<tr>
<td>( g )</td>
<td>14.18 (33.29)</td>
<td>1.98 (2.34)</td>
<td>2.71 (1.03)</td>
</tr>
<tr>
<td>( c )</td>
<td>0.00 (0.13)</td>
<td>0.32 (0.24)</td>
<td>0.74 (0.25)</td>
</tr>
<tr>
<td>( a' ) (m(^2)/hr)</td>
<td>0.005</td>
<td>0.05</td>
<td>0.06</td>
</tr>
<tr>
<td>( a_k ) (m(^2)/hr)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( k=0 )</td>
<td>0.0027 (0.009)</td>
<td>0.0078 (0.008)</td>
<td>0.02</td>
</tr>
<tr>
<td>( k=1 )</td>
<td>0.0</td>
<td>0.0048 (0.014)</td>
<td>0.11</td>
</tr>
<tr>
<td>( k=2 )</td>
<td>-</td>
<td>0.0039 (0.023)</td>
<td>0.02</td>
</tr>
<tr>
<td>( k=3 )</td>
<td>-</td>
<td>0.043 (0.10)</td>
<td>0.02</td>
</tr>
<tr>
<td>( k=4 )</td>
<td>-</td>
<td>0.0 (0.083)</td>
<td>0.05</td>
</tr>
<tr>
<td>( k=5 )</td>
<td>-</td>
<td>-</td>
<td>0.01</td>
</tr>
</tbody>
</table>
increased. Her explanation for the decrease in search rates, based on observations of sculpin behaviour in her experimental enclosures, was that larger sculpins tended to be much less active than smaller ones. She suggested that larger sculpins were preferred as prey by fish-eating birds and thus that predator avoidance overwhelmed their interest in feeding. These observations were made during daylight, whereas my experiments took place mainly at night. At night, avian predation would be less of a concern, so that size related differences in sculpin activity would not be as likely to occur.

5.3 Prey Size

Since prey size was not rigidly controlled in the 1979 experiments, a fairly wide range of prey sizes were available to predators, particularly later in the spring when a wider range of prey sizes were present naturally in the estuary. To assess whether prickly sculpins prey more heavily on certain sizes of fry than others I have compared the mean lengths of those fry that were eaten and those that escaped predation. Since these experiments only lasted 4-5 hr all consumed fry were still quite fresh and therefore easy to measure.

Two criteria must be met for an analysis of this type to be valid. First, enough fry must be consumed by sculpins to allow a sufficient sample size for a reasonably precise
estimate of mean lengths of consumed prey. Second, the total number of fry eaten by all sculpins in an experiment must comprise a small proportion of the total number of fry available. If this second condition is violated, the two samples (eaten and uneaten) cannot be independent, and any differences between the two will be exaggerated.

To ensure that both of these criteria were met, I analysed only the results from the two highest density experiments (640 prey). In these two cases the average number of fry consumed per predator was relatively large (6.18) while the proportion consumed was quite small (<10%). Students t-tests comparing the mean length of a random sample of 20 recaptured (not eaten) fry to the mean length of fry in individual predator stomachs (Table 10) offer no evidence of size selective predation. This supports my seventh prediction, although it could be that encounter rates increase with prey size due to the greater swimming speed of larger fry, but that this is countered by a decrease in capture success. For sculpins much smaller than those used in this analysis, my laboratory observations would suggest a more significant prey size effect, due to poorer capture success on larger fry.

5.4 Abiotic Factors

The two abiotic factors discussed in Chapter 2, turbidity and temperature, were not experimentally addressed in
Table 10. Results of t-tests to compare the mean lengths of fry consumed by sculpins to the mean length of fry exposed to sculpin predation in functional response experiments (L). Fry consumed by seven sculpins were examined from each of two experiments. For both experiments, 640 fry were added to the enclosure. The mean length of fry that escaped predation was computed from a subsample (N) of 20 fish from each experiment. None of the t-values presented in this table are significant at α = 0.05.

1. Experiment #1: May 28, 1979

\[ \bar{L} = 36.2 \text{ mm; } S_L = 3.56; \ N = 20 \]

<table>
<thead>
<tr>
<th>SCULPIN #</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
</tr>
</thead>
<tbody>
<tr>
<td># prey eaten (n)</td>
<td>10</td>
<td>4</td>
<td>10</td>
<td>8</td>
<td>11</td>
<td>6</td>
<td>4</td>
</tr>
<tr>
<td>mean length (( \bar{I} ))</td>
<td>34.7</td>
<td>35.7</td>
<td>34.9</td>
<td>35.4</td>
<td>34.7</td>
<td>36.0</td>
<td>36.2</td>
</tr>
<tr>
<td>std. error (( s_{\bar{I}} ))</td>
<td>2.67</td>
<td>3.34</td>
<td>2.99</td>
<td>3.30</td>
<td>4.30</td>
<td>4.01</td>
<td>3.02</td>
</tr>
<tr>
<td>deg. freedom</td>
<td>28</td>
<td>22</td>
<td>28</td>
<td>26</td>
<td>29</td>
<td>24</td>
<td>22</td>
</tr>
<tr>
<td>( t_{\text{calc}} )</td>
<td>.918</td>
<td>.134</td>
<td>.755</td>
<td>.375</td>
<td>.725</td>
<td>.069</td>
<td>.000</td>
</tr>
</tbody>
</table>

2. Experiment #2: May 29, 1979

\[ \bar{L} = 40.4 \text{ mm; } S_L = 4.27; \ N = 20 \]

<table>
<thead>
<tr>
<th>SCULPIN #</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
</tr>
</thead>
<tbody>
<tr>
<td># prey eaten (n)</td>
<td>10</td>
<td>4</td>
<td>7</td>
<td>12</td>
<td>2</td>
<td>3</td>
<td>5</td>
</tr>
<tr>
<td>mean length (( \bar{I} ))</td>
<td>40.0</td>
<td>40.2</td>
<td>38.5</td>
<td>38.3</td>
<td>39.6</td>
<td>43.9</td>
<td>39.3</td>
</tr>
<tr>
<td>std. error (( s_{\bar{I}} ))</td>
<td>3.50</td>
<td>6.53</td>
<td>3.90</td>
<td>3.45</td>
<td>1.27</td>
<td>1.63</td>
<td>4.43</td>
</tr>
<tr>
<td>deg. freedom</td>
<td>28</td>
<td>22</td>
<td>25</td>
<td>30</td>
<td>20</td>
<td>21</td>
<td>23</td>
</tr>
<tr>
<td>( t_{\text{calc}} )</td>
<td>.164</td>
<td>.031</td>
<td>.563</td>
<td>.990</td>
<td>.081</td>
<td>-.545</td>
<td>.238</td>
</tr>
</tbody>
</table>
this study, and thus no specific results are available. Both were monitored during the Fraser estuary experiments, and I carried out multiple regressions with temperature and turbidity as independent variables, and either number of attacks, or the residuals from the best fit functional response curve (Fujii model), as the dependent variable. Neither abiotic variable was able to explain a significant amount of the actual, or residual variation in rates of attack.

It is quite possible that the contrast in turbidity in the Fraser estuary is insufficient to result in a measurable effect of this parameter on predation rates. The contrast between the Fraser estuary and Rosewall Creek is much more substantial. Comparisons of these two systems are confounded, however, by differences in other key variables, most notably alternate prey. On the other hand, my laboratory observations suggest that sculpin predation is characterized by an ambush mode of feeding, which would make it unlikely that turbidity plays a major role in influencing predation rates.
VI POPULATION LEVEL CONSEQUENCES OF PREDATION

The principal motivation for conducting the research presented in this thesis was to provide a defensible basis for estimating the impact (in terms of mortality) of prickly sculpin predation on seaward migrating chum salmon fry. My premise was that to achieve this objective, one needed to understand the form and magnitude of the sculpin functional response to their prey, and have some idea of the influence on the functional response of other factors, both biotic and abiotic. While I would argue that these are necessary ingredients of a defensible impact estimate, they are obviously not sufficient. One also needs to have information on the abundance of both the predator and the prey. Further, where conditions that influence predation vary spatially within the system of interest (such as the abundance of alternate prey), the distribution of both predator and prey become important. In this Chapter, I integrate my experimental results with my own field observations and with data from other sources, to examine at each of my study sites the potential mortality imposed on chum fry by prickly sculpins.

6.1 Fraser Estuary

6.1.1 Analytical Methods

In estimating predation impacts in the Fraser estuary,
I have focussed on two major tidal channels of Woodward Island (W1 and W2: see Figure 7). W1 channel was the site of my field experiments in the Fraser estuary, and all my sculpin trap sites associated with marsh habitat were either within these two channels or along the marsh edge between them. The two channels comprise a total area of 28,700 m$^2$. I have assumed that within this area all factors that influence predation are effectively homogeneous (e.g., prey and predator densities, alternate prey abundance). In the following paragraphs I describe the calculations and other assumptions I have used to arrive at predation mortality estimates. There are three major steps involved: estimating daily predator abundance; estimating daily prey densities; and applying the functional response to these estimates.

In 1980, I attempted to obtain prickly sculpin abundance estimates using mark-recapture methods. Unfortunately, excessive tag losses during the four month field season made it impossible for me to obtain accurate estimates. Tag losses will result in underestimates of the total numbers of sculpins recaptured during the sampling period. Therefore, a population estimate based on these data will tend to overestimate the true population size, unless a large proportion of the population is not vulnerable to the gear used. The sculpin population estimate derived from my 1980 mark-recapture data should thus be considered an upper bound on their abundance. I used a Bayesian method (Gazey and Staley, in press) to arrive at this estimate. Other methods
(e.g., Schnabel, Schumacher/Eschmayer) yielded similar results, but the Bayesian method is purportedly less biased for small numbers of recaptures.

No fish tagged in the slough habitat (away from the marsh edge) were ever recovered in marsh edge or tidal channel traps. Therefore, I have assumed these two populations are distinct, such that it is possible to derive population estimates for the marsh edge and tidal channel fish alone. For the purposes of estimating maximum potential predation impact I have also assumed that the entire sculpin population in these two latter areas actually utilize the channels for feeding when they are not dewatered.

Catch per unit effort data from my traps suggest that sculpin abundance in these areas was not constant throughout the fry migration period (Figure 21). To generate estimates of the daily sculpin abundance during this period, I combined these data with the maximum abundance estimate obtained from the mark-recapture analysis. The Bayesian estimation procedure computes abundance estimates for each sampling date, and the maximum of these estimates corresponded to the time of greatest catch per effort. Therefore, I assumed that the maximum population estimate reflected the day on which the maximum catch per effort was observed, and that the trap catchability was constant and independent of sculpin abundance. Thus the number of sculpins present on any given day "i" that trap data were gath-
Figure 21. Upper panel: Temporal pattern of sculpin catches from traps set in the tidal channel and marsh edge habitat of Woodward Island in the Fraser estuary. Lower panel: Estimated temporal pattern of chum fry densities in Woodward Island tidal channels (data from Levy and Northcote 1981).
erected is given by:

\[ N_i = N_M \cdot \frac{(C/f)_i}{(C/f)_M} \quad (24) \]

where \( N_i \) = number of sculpins on day \( i \);
\( N_M \) = maximum sculpin population estimate;
\( (C/f)_i \) = catch per effort on day \( i \); and
\( (C/f)_M \) = maximum catch per effort.

To estimate sculpin numbers on days when trap data were not gathered I interpolated between the closest sampling day before and after this date.

I did not attempt to estimate chum fry densities in this study. Estimates are available from Levy and Northcote (1981) for tidal channel W1 in 1979, however. I have used these data and again interpolated between sampling dates to estimate densities on non-sampling days.

As well as daily fry density estimates I also needed an estimate of the total number of fry using the tidal channels during the migration period (March-June). This value can be estimated from Levy and Northcote's (1981) data, but depends critically on the assumed residence time of fry in the area. There are no good estimates of this for the Fraser estuary, although in 1978 and 1979 Levy and Northcote (1981) observed a very low recapture rate (zero in 1979) for marked chum fry
released into W1 and W2 channels for approximately one week. As well, they observed very little change in the sizes of chum fry until mid-May, relative to fry collected upstream in the Fraser river at Mission. This would suggest a relatively short residence time for the fry, since estuarine growth is normally quite rapid (Healey 1979). In the Nanaimo estuary, Healey (1979) estimated residency times of 0-18 days for chum fry (less than ten days for most of the migration period). I have estimated total numbers using assumed residency times ranging from 1 to 13 days.

To apply a functional response I have used parameter estimates for the Fujii model (Table 5). The Fujii model cannot be applied directly since the handling time estimates assume a value of $T_t$ equal to 4.5 hours. The tidal channels of interest are flooded for approximately 50% of the time each day. Thus a more reasonable estimate of $T_t$ is 12 hours. This assumes that sculpins feed throughout the day and night, which is probably true in the turbid waters of the Fraser estuary. At high prey densities, this change will not be important, since the sculpins will obtain their maximum ration regardless of $T_t$. When prey are scarce, however, the time available for feeding will have an important influence on predation rates. To accommodate this I have divided the Fujii model into two components. First the potential prey
consumption per predator is calculated from

\[ A_p = a' \cdot \exp(c \cdot N_o) \cdot N_o \cdot T_t \]  

(25)

where \( A_p \) = potential prey consumption;
\( a' \) = rate of effective search;
\( c \) = Fujii c parameter;
\( N_o \) = prey density; and
\( T_t \) = time available for feeding.

Then the actual consumption per predator \((A_o)\) is given by the lesser of \( A_p \) and \( A_{\text{max}} \). The net effect is a functional response similar in form to a Type I response, at least when \( c=0 \). I have estimated predation rates for Fujii model parameters from both 1979 (high density treatments excluded) and 1980.

My laboratory observations of sculpin feeding patterns suggested that sculpins spend at least one full day digesting a meal. Typically, sculpins fed to satiation ceased further feeding for one to two days. This implies that predation on any given day is not independent of the previous day's feeding success. As a first approximation, I have accounted for this by removing from the predator population for one day, those predators that either fed (alternative A) or fed to satiation (alternative B) on any given day. In my experiments, the distribution of attacks among sculpins did not differ significantly from a Poisson distribution at most prey densities and in all years (Table 11). Based on a Pois-
Table 11. Results of goodness-of-fit tests of the functional response data to a Poisson distribution. The tests are based on a calculated chi-squared:

\[ \chi^2 = \sum \frac{(O_i - E_i)^2}{E_i} \]

where \( i \) = number of attacks per predator per experiment; 
\( O_i \) = number of observations of \( i \) attacks; and 
\( E_i \) = expected number of attacks, given a Poisson distribution around the observed mean number of attacks.

<table>
<thead>
<tr>
<th>Year</th>
<th>Prey Density</th>
<th>Observed Proportion of Zero Attacks</th>
<th>Expected* Proportion of Zero Attacks</th>
<th>( \chi^2 )</th>
<th>df</th>
<th>prob(( \chi^2 ))</th>
</tr>
</thead>
<tbody>
<tr>
<td>1979</td>
<td>20</td>
<td>0.625</td>
<td>0.687</td>
<td>.474</td>
<td>1</td>
<td>&gt; .3</td>
</tr>
<tr>
<td></td>
<td>40</td>
<td>0.455</td>
<td>0.135</td>
<td>12.69</td>
<td>4</td>
<td>&gt; .01</td>
</tr>
<tr>
<td></td>
<td>80</td>
<td>0.143</td>
<td>0.102</td>
<td>3.86</td>
<td>5</td>
<td>&gt; .5</td>
</tr>
<tr>
<td></td>
<td>160</td>
<td>0.333</td>
<td>0.089</td>
<td>14.22</td>
<td>5</td>
<td>&gt; .01</td>
</tr>
<tr>
<td></td>
<td>320</td>
<td>0.176</td>
<td>0.012</td>
<td>51.89</td>
<td>7</td>
<td>&lt; .001</td>
</tr>
<tr>
<td></td>
<td>640</td>
<td>0.000</td>
<td>0.002</td>
<td>11.38</td>
<td>9</td>
<td>&gt; .2</td>
</tr>
<tr>
<td>1980</td>
<td>20</td>
<td>0.737</td>
<td>0.692</td>
<td>1.59</td>
<td>2</td>
<td>&gt; .3</td>
</tr>
<tr>
<td></td>
<td>40</td>
<td>0.550</td>
<td>0.472</td>
<td>.871</td>
<td>2</td>
<td>&gt; .5</td>
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<tr>
<td></td>
<td>80</td>
<td>0.517</td>
<td>0.355</td>
<td>5.73</td>
<td>3</td>
<td>&gt; .1</td>
</tr>
<tr>
<td></td>
<td>160</td>
<td>0.350</td>
<td>0.183</td>
<td>8.32</td>
<td>4</td>
<td>&gt; .05</td>
</tr>
<tr>
<td>1981</td>
<td>20</td>
<td>0.267</td>
<td>0.119</td>
<td>6.61</td>
<td>4</td>
<td>&gt; .1</td>
</tr>
<tr>
<td></td>
<td>40</td>
<td>0.167</td>
<td>0.054</td>
<td>6.48</td>
<td>5</td>
<td>&gt; .2</td>
</tr>
<tr>
<td></td>
<td>80</td>
<td>0.091</td>
<td>0.071</td>
<td>.710</td>
<td>5</td>
<td>&gt; .98</td>
</tr>
<tr>
<td></td>
<td>160</td>
<td>0.167</td>
<td>0.125</td>
<td>3.17</td>
<td>4</td>
<td>&gt; .5</td>
</tr>
<tr>
<td></td>
<td>320</td>
<td>0.000</td>
<td>0.003</td>
<td>1.69</td>
<td>3</td>
<td>&gt; .5</td>
</tr>
</tbody>
</table>

* - cells with less than five expected attacks were lumped into adjacent cells.

* - expected proportion of zero attacks is calculated from \( p(0) = e^{-X} \), where \( X \) is the mean number of attacks at that prey density.
son distribution, the proportion of sculpins that feed on a particular day \( p_f \) is given by:

\[
1 - \exp(-A_o)
\]

Similarly, the proportion that feed to satiation on each day \( p_C \) is given by:

\[
\frac{(A_{max} - 1) A_o^i \cdot \exp(-A_o)}{1 - \sum_{i=0}^{i!}}
\]

6.1.2 Results

The total prey consumption estimates presented in Table 12, when compared to estimates of total fry utilization of the tidal channels, cannot be considered insignificant. Overall percent mortality estimates range from 6-81%, depending the combination of functional response and residency time assumptions chosen. The importance of residency time is made obvious by this analysis, emphasizing the critical need for improved estimates of this parameter. Both the functional response parameters and the alternative chosen to describe the temporal feeding pattern of sculpins also have pronounced effects on impact estimates, but to a
Table 12. Predation estimates for prickly sculpins feeding on chum fry in two tidal channels in the Fraser estuary.

Estimated maximum sculpin abundance: 6950 (0.24/m²)
Estimated maximum fry density: 0.90/m²

<table>
<thead>
<tr>
<th>TIME (DAYS)</th>
<th>RESIDENCY TOTAL NUMBERS</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>448,568</td>
</tr>
<tr>
<td>2</td>
<td>247,385</td>
</tr>
<tr>
<td>4</td>
<td>130,317</td>
</tr>
<tr>
<td>6</td>
<td>88,704</td>
</tr>
<tr>
<td>8</td>
<td>80,960</td>
</tr>
<tr>
<td>10</td>
<td>73,934</td>
</tr>
</tbody>
</table>

Results of predation estimates:

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>maximum daily percent mortality</td>
<td>35.4</td>
<td>26.7</td>
<td>44.4</td>
<td>29.1</td>
</tr>
<tr>
<td>total fry consumed by sculpins</td>
<td>27,648</td>
<td>39,740</td>
<td>51,555</td>
<td>59,568</td>
</tr>
</tbody>
</table>
lesser degree than residency time. Whichever feeding assumptions are chosen, a relatively long residency time (e.g., 10 days) yields an impact estimate in excess of 35%, whereas a single day residency implies an impact no greater than 15%.

While these results suggest that sculpin predation on fry may be an important source of mortality, the predation estimates in Table 12 are probably upper bounds on the impact of sculpins on chum fry in these tidal channels. As mentioned earlier, tag losses are probably responsible for overestimates of sculpin abundance. Also, alternate prey are not explicitly considered in these estimates, although their effect is at least partially implicit in the functional response parameter estimates.

Estimated sculpin densities are comparable to those for chum fry except at the peak densities for the latter (Figure 21). This is in contrast to the observations of Levy et al. (1979), who caught very few large prickly sculpins (relative to salmon fry) while sampling these channels for fish. While gear avoidance by sculpins might be implicated as explaining this anomaly in part, it seems highly unlikely that their catches would have been so small if prickly sculpins were comparable in abundance to chum fry. The sculpin densities assumed here (up to 6950/28700 per m$^2$) may high due to errors in both the overall population estimates and in the assumption that all sculpins occupy the tidal channels when they are flooded.
There are no studies reported in the literature of sculpin abundance in habitats similar to those sampled in the Fraser estuary. In other habitats, however, abundances of sculpins are of the same order of magnitude as the estimates used here. Hunter (1959) estimated densities of *Cottus asper* and *C. aleuticus* ranging from .13-.31/m² in Hooknose Creek. Mason and Machidori (1976) observed biomass densities of the same species in small coastal streams sampled in mid-summer and autumn to range from 2-6g/m². For predatory-sized fish, this probably implies densities well below 1/m². In contrast, Eggers *et al.* (1978) found densities of age 1+ and older *C. asper* in excess of 2.4/m² in Lake Washington. Similarly, my abundance estimates from Rosewall Creek suggest densities of predatory-sized fish exceeding 2/m², although virtually all of these fish are smaller than those captured in the Fraser estuary. Finally, Finger (1982) and Anderson (1985) have observed densities of *Cottus* sp. in freshwater systems ranging from 1-2/m² and .01-1.3/m², respectively. These data suggest that my estimates of sculpin abundance in the Fraser estuary tidal channels are not unrealistically high.

Two classes of alternate prey may influence sculpin predation on chum fry: other salmon fry and invertebrates. Other salmon fry become abundant in the estuary at the same time as chum fry (chinook, pink every second year). At the peak of the chum fry migration, prey densities are sufficiently high to nearly swamp the predator; the additional
effect of other, similar prey should be to dilute the impact of sculpin predation on chum fry. As well, I presented data earlier that indicated significant variations in invertebrate prey abundance during the spring. The functional response parameter estimates for each year can be thought of as averaging this variability in invertebrate prey abundance. If the peak in invertebrate prey abundance more or less coincides with that for chum fry, the impact of sculpins on chum fry may be considerably reduced.

To conclude this discussion, it is useful to consider the significance of these estimates in the context of the tidal marshes of the Fraser estuary as a whole. Levy et al. (1979) and Levy and Northcote (1981) sampled tidal channels at a number of locations in the estuary, and found densities of chum fry to be at least as great on Woodward Island as at any other site. Thus one might consider the Woodward Island channels to offer particularly important habitats for seaward migrating chum fry. On the other hand, my estimates of total fry utilization of these two channels are very small relative to the estimated total downstream migration of chum fry in 1979 (approximately 88,000,000: Levy and Northcote 1981) on the Fraser river, even for an assumed residency of only one day. If one assumes that the majority of these fry spend some time in habitats similar to those on Woodward Island, then the potential impact of prickly sculpins on chum fry populations cannot be considered insignificant. Clearly the degree of utilization of these habitats by chum
fry, and the abundance of sculpins within them, remain important research questions for the future.

6.2 Rosewall Creek

Examination of sculpin predation impacts on chum fry at Rosewall Creek focuses on the side-channel used for my functional response experiments at this site (Figure 8). The mark-recapture studies were more successful here than in the Fraser estuary, so more plausible predator abundance estimates can be used in this analysis. These abundance data, together with information I collected on the spatial distribution of sculpins and their feeding habits, allow a more thorough examination of the interaction between sculpins and chum fry. Data on chum fry abundance, however, are not available for this system. I have relied instead on information from another small coastal stream, Hooknose Creek, where chum salmon-sculpin interactions have been previously examined (Hunter 1959). I have developed a simple model that allows one to explore the interaction between the density (and temporal pattern of emergence) of fry and sculpin predation in a small coastal stream, of which Rosewall Creek serves as an example. Analysis of this model allows me to quantitatively address certain key questions concerning the sculpin-salmon interaction:

1) given the functional response parameter and predator abundance estimates obtained in this study,
how does the impact of sculpin predation on chum fry vary with fry density? This question is of obvious relevance to the issue of how chum salmon populations subjected to sculpin predation will respond to enhancement efforts that increase fry densities;

2) how does the rate of movement of fry downstream, a parameter about which there is considerable uncertainty, affect this interaction between fry abundance and predation rate?

3) how important are alternate prey in reducing the impact of sculpin predation on chum fry?; and

4) what is the effect of changes in the timing of fry emergence on this interaction?

5) which size class(es) of sculpin exert the greatest impact on chum fry?

In the model, the stream is divided into a number of reaches (three for the example of the Rosewall Creek experimental channel). Each stream reach is considered homogeneous and is characterized by a number of physical and biological features, discussed below, such as surface area and predator densities. The model simulates the entire period of emergence of fry anywhere in the stream. Each day within this period is disaggregated into hourly intervals during which
fry emerge and move downstream. The model can be described by three relationships:

\[ T_E = \sum_{t} \sum_{r} A_{r,t} \cdot \tau \]

\[ A_{r,t} = f(N_{o_r,t}, T_t, AP_r) \quad \{ \text{functional response} \} \quad ; \quad (26) \]

\[ N_{o_r,t} = N_{o_r,t-1} + \left[ e_{r,t-1} + u_{r,t-1} - d_{r,t-1} - P_{r,t-1} \cdot A_{r,t-1} \right] / S_r. \]

where \( T_E \) = total fry eaten per day;
\( t \) = hour index;
\( r \) = reach index;
\( P \) = predator numbers;
\( A \) = fry eaten per predator;
\( N \) = fry density (#/m);
\( T_t \) = time available for feeding;
\( AP \) = alternate prey abundance;
\( e \) = number of fry emerging;
\( u \) = number of fry entering from upstream;
\( d \) = number of fry moving downstream; and
\( S \) = area of stream reaches.

Using information on the distribution and abundance of sculpins, chum fry and alternate prey, and on the functional response, the model predicts the total number of fry consumed by sculpins, and the overall percent mortality due to predation, throughout the fry migration period.
6.2.1 Predator Abundance and Distribution

Since at Rosewall Creek marking was by fin removal, rather than tagging, there were no problems with tag losses. Laboratory observations of marked fish revealed no evidence of mortality or of fin regeneration throughout the period of the mark-recapture study. While the two sampling areas were separated by less than 0.2 km, there was no indication of any movement of sculpins between areas. This is in contrast to the observations of others (Hunter, 1959; Krejsa, 1967), but may be a consequence of their looking at movements on a larger spatial scale. Krejsa (1967) suggests that prickly sculpins typically undergo a downstream migration in the early spring to spawn in or near the estuary. My field observations may have been confined only to sculpins which had already reached the downstream limit of their spring movements. Based on my own observations, I assume in the model that sculpins do not move between reaches.

Population estimates derived from the Bayesian closed population multiple census model (Gazey and Staley in prep) indicate the sculpins are approximately three to four times as abundant in the estuary as in freshwater (Table 13). This difference is corroborated by catch per unit effort data (Figure 22) which demonstrate a strong tendency for sculpins to concentrate in estuarine habitats offering plenty of cover.

To account for predator size effects in the model, I
Table 13. Sculpin abundance estimates and the size-frequency distribution of the trap catch for the Rosewall Creek experimental channel.

<table>
<thead>
<tr>
<th></th>
<th>RIVER SITES</th>
<th>ESTUARY SITES</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bayesian abundance estimate</td>
<td>318</td>
<td>1108</td>
</tr>
<tr>
<td>5th and 95th percentiles</td>
<td>262-406</td>
<td>988-1252</td>
</tr>
<tr>
<td>Proportion of total catch:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>60-100 mm</td>
<td>.82</td>
<td>.84</td>
</tr>
<tr>
<td>100-140 mm</td>
<td>.16</td>
<td>.15</td>
</tr>
<tr>
<td>&gt; 140 mm</td>
<td>.02</td>
<td>.01</td>
</tr>
</tbody>
</table>
Figure 22. Temporal pattern of sculpin catch per unit effort from traps set in four habitats in the experimental channel of Rosewall Creek.
apportion the total abundance figures to three size categories (60-100 mm, 100-140 mm, > 140 mm total length), using the observed size-frequency distribution of the catch (Table 13). The "river" population estimate applies to the uppermost reach in the model, and I assume similar predator densities in the second reach. The "estuary" population estimate applies to the lowest stream reach.

6.2.2 Prey Abundance and Distribution

The prey density at any point in space and time is the consequence of three processes: emergence, downstream movement of fry and predation (equation 26). For the uppermost reach the "u" term is zero (at Rosewall Creek, the experimental channel was not connected to the main channel except by subsurface flow, so it was assumed that no fry were entering from upstream), while the "d" term for the lowest reach defines the fry escapement from the system.

Emergence rates in each stream reach are calculated from a spawning population estimate, fecundity, egg to emergence survival and a specified diurnal and seasonal pattern of swim up. Spawning densities are assumed to be uniform across all stream reaches, as are fecundity, egg to emergence survival rates, and emergence timing patterns. Based on the data from Hooknose Creek, I have assumed that the seasonal pattern of emergence follows a symmetrical distribution, which I have approximated using a normal
distribution. Emergence is assumed to commence at 2100 hr and continue until 0500 hr the following day. The proportion of the daily emergence of fry that swim up in each hour is not constant, but rather follows a pattern whereby most emergence occurs in the earlier hours of the night. The parameters that describe spawning and emergence in the model are summarized in Table 14.

The downstream movement rates of fry determine the duration of exposure of individual fry to predation. Fry movement rates have been discussed elsewhere in this thesis; there is considerable uncertainty about the value of this parameter. It is often assumed that chum fry move downstream with the current immediately upon emergence (e.g., Hunter 1959). Observations of fry in Rosewall Creek at night, however, did not indicate a rapid downstream passage. Rather, periods of downstream drifting were interspersed with "holding" periods during which fry maintained their position in the current or moved laterally across the stream. As a starting point, I have assumed a net downstream movement rate of 1 cm/sec (approximately 0.3 body lengths per second). Assuming a uniform distribution of fry throughout each stream reach, the proportion of fry in a reach that move into the next lowest reach in an hour is given by the quotient of the distance moved by fry in an hour and the length of the stream reach.
Table 14. Input parameter values for the simulation of sculpin predation on chum fry in the Rosewall Creek experimental channel.

Stream reach dimensions:

<table>
<thead>
<tr>
<th>Reach</th>
<th>Length (m)</th>
<th>Width (m)</th>
<th>Area (m²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>75</td>
<td>2</td>
<td>150</td>
</tr>
<tr>
<td>2</td>
<td>100</td>
<td>3</td>
<td>300</td>
</tr>
<tr>
<td>3</td>
<td>250</td>
<td>4</td>
<td>1000</td>
</tr>
</tbody>
</table>

Chum spawning and emergence:

- Fecundity: 2500 eggs/female
- Egg-emergence survival: 10%
- Length of emergence period: 60 days
- Standard deviation of emergence distribution: 10.0

Diurnal pattern of emergence

<table>
<thead>
<tr>
<th>Hour</th>
<th>Proportion emerging</th>
</tr>
</thead>
<tbody>
<tr>
<td>2100</td>
<td>0.05</td>
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<tr>
<td>2200</td>
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<td>0.01</td>
</tr>
<tr>
<td>0600-2000</td>
<td>0.00</td>
</tr>
</tbody>
</table>
6.2.3 Functional Response

Given estimates of prey and predator densities for each stream reach, predation rates can be calculated from the results of my functional response experiments. The Fujii model parameters (1981 data) are used in exactly the same fashion as was described for the Fraser estuary, except that $A_p$ is calculated each hour, and then accumulated over a 24 hour period. The model accounts for predator digestive pause in the same fashion as well, although for the results presented below only alternative B is employed. This alternative will always lead to higher predation estimates than alternative A. The choice of alternative should not affect the qualitative behaviour of the model discussed below.

In contrast to the Fraser estuary case, I have assumed that sculpins only feed at night in the Rosewall Creek example. My investigation of the temporal distribution of sculpin activity (as measured by trapping success) revealed that while approximately 42% of the time that the traps were sampling was during the day, only 6.4% of the total catch occurred during this period. In addition, the only fish caught during the day were recovered from traps nearest protective cover. A more intensive examination of sculpin activity during the night only (same metric) revealed no striking differences in activity at different times (Table 15). Therefore, I have assumed the value of $T_t$ to be 9 hours for the model analyses presented below, which is
Table 15. Sculpin catches in minnow traps set in the Rosewall Creek experimental channel and checked at four times during the period from dusk to dawn.

<table>
<thead>
<tr>
<th>TIME INTERVAL</th>
<th>CATCH PER HOUR SAMPLED</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>mean</td>
</tr>
<tr>
<td>1800-2000</td>
<td>2.00</td>
</tr>
<tr>
<td>2000-2200</td>
<td>4.02</td>
</tr>
<tr>
<td>2200-0400</td>
<td>2.10</td>
</tr>
<tr>
<td>0400-0600</td>
<td>2.00</td>
</tr>
</tbody>
</table>

ANOVA table to test for significant differences among means*

<table>
<thead>
<tr>
<th>SOURCE</th>
<th>df</th>
<th>SS</th>
<th>MS</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total</td>
<td>19</td>
<td>66.38</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Among</td>
<td>3</td>
<td>14.78</td>
<td>4.93</td>
<td>1.53</td>
<td>&gt; 0.05</td>
</tr>
<tr>
<td>Within</td>
<td>16</td>
<td>51.60</td>
<td>3.23</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* Bartlett's test indicated no significant differences among sample variances.
approximately equal to the length of night at this time of year.

Finally, the results of my experiments in both Rosewall Creek and the Fraser estuary suggest that alternate prey have an important influence on sculpin predation. Invertebrate alternate prey were clearly far more abundant in the estuary reach than in the two freshwater reaches, as evidenced by the ease with which these prey were collected by "kick sampling" for my alternate prey experiments, and by the much higher incidence of sculpin feeding on chum fry in the freshwater reaches (Table 16). Sculpins collected in the estuary appeared to be obtaining at least as much food as those collected in freshwater (Table 16), but invertebrates dominated the diet of the former group. These observations are consistent with my alternate prey experiments, in which consumption rates of chum fry decreased by 60-90% when alternate prey were made available. On the basis of the assumption that this result is a consequence of alternate prey causing a reduction in the rates of effective search of sculpins for chum fry (see Chapter 2), I have reduced the search rates for all sizes of sculpin by 80% in the lowest reach, to account for the presence of alternate prey in this area.

6.2.4 Results

To analyze the model, I have carried out a number of
Table 16. Stomach contents data for sculpins collected at four trapping sites in the Rosewall Creek experimental channel.

<table>
<thead>
<tr>
<th>TRAPPING SITES</th>
<th>RIVER</th>
<th>ESTUARY</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>OPEN</td>
<td>COVER</td>
</tr>
<tr>
<td>Number of fish examined</td>
<td>121</td>
<td>49</td>
</tr>
<tr>
<td>Number with fry in stomachs</td>
<td>42</td>
<td>19</td>
</tr>
<tr>
<td>Proportion with fry in stomachs</td>
<td>.347</td>
<td>.388</td>
</tr>
<tr>
<td>Number of fry consumed per sculpin</td>
<td>.793</td>
<td>.837</td>
</tr>
<tr>
<td>Number of fry consumed per sculpin with fry</td>
<td>2.29</td>
<td>2.11</td>
</tr>
<tr>
<td>Mean stomach contents index</td>
<td>1.35</td>
<td>1.43</td>
</tr>
<tr>
<td>Mean stomach contents index for sculpins without fry</td>
<td>.797</td>
<td>.766</td>
</tr>
<tr>
<td>Proportion with empty stomachs</td>
<td>.248</td>
<td>.265</td>
</tr>
</tbody>
</table>
simulations in which I vary the abundance of spawning adult fish from 50 to 1000. This corresponds to an areal density of spawning chum salmon ranging from 0.09 to 1.82 per square meter. Hunter (1959) observed spawner densities ranging from 0.04 to 0.55 per square meter, with a mean of 0.16. Other investigators have found optimum spawning densities for chum salmon to be approximately 0.22 per square meter of suitable substrate (Reiser and Bjornn (1979); this figure would presumably be reduced by correcting for the proportion of stream bottom area that provides suitable substrate. While the maximum spawner densities simulated might therefore seem exceedingly high, they will yield fry densities that are conceivable in artificial (hatchery, spawning channel) situations.

Seven sets of simulations have been used to examine the five questions listed earlier in this section (Table 17). The results are presented as plots of total percent mortality of fry due to predation versus spawner abundance (Figure 23). Total percent mortality is computed from:

\[ TM = \frac{\sum_{t} d_{3,t}}{(\sum_{r} \sum_{t} e_{r,t})}. \]  

(27)

Considering first the baseline scenario, the increasing trend in percent mortality with increasing spawner abundance indicates that the fry are not "swamping" their predators,
Table 17. Descriptions of the seven scenarios run on the model of sculpin predation on chum fry in the Rosewall Creek experimental channel, and depicted in Figure 23.

1. **Baseline.** Parameters set as discussed in the text or presented in Tables 13 and 14.

2. **Fry Movement Rate.** The average rate of downstream movement of fry is reduced from 1.0 cm/sec to 0.25 cm/sec.

3. **Alternate Prey.** The effect of alternate prey in reach 3 is removed. For the baseline, the model assumes alternate prey in reach 3 reduce sculpin search rates by 80%.

4. **Emergence Pattern.** The standard deviation of the normal distribution used to simulate daily fry emergence is reduced from 10.0 to 2.5. This has the effect of greatly reducing the period over which most of the fry emerge and move downstream.

5. **Large Sculpins.** The density of sculpins in the > 140 mm size class is reduced to zero.

6. **Small Sculpins.** The density of sculpins in the 60-100 mm size class is reduced to zero.

7. **Medium Sculpins.** The density of sculpins in the 100-140 mm size class is reduced to zero.
Figure 23. Results of the Rosewall Creek sculpin predation model. Overall percent mortality of chum fry due to sculpin predation is plotted as a function of the number of spawning adults from the previous fall. Results are plotted for each of the seven scenarios discussed in the text and briefly described in Table 17. The numbers identifying each curve correspond to those in Table 17.
at least until very high spawner abundance levels are reached. The maximum percent mortality is actually observed at a spawner density of 1.36 per square meter (750 fish). This suggests that efforts to increase fry output will be thwarted by increases in predation by sculpins. Predation rates are relatively low at all densities, however, and the increase in percent mortality does not come close to compensating entirely for the increased fry production. In this instance increasing the number of spawners by a factor of 10 (50 to 500) resulted in an increase of only 1.68% in mortality rates (5.28 to 6.96).

Reducing the movement rate of fry, and removing the effect of alternate prey in the lowest reach, both had pronounced effects on predation rates. At realistic natural spawner densities, predation rates were approximately 2.5 times as great when these changes were made. Also in these two scenarios there is a clear indication of predator swamp ing at much lower prey densities than in the baseline.

Here, as in the Fraser estuary, the residence time of fry in the system proves to be a critical parameter, about which there is insufficient knowledge. If the fry move out of the system rapidly, as is often assumed, then the potential for predation impacts in freshwater is greatly reduced.

The model results emphasize the importance of alternate prey to the sculpin-salmon fry interaction. It suggests that changes in the abundance of alternate prey may have a far greater impact on chum fry than will changes in their own
density. While the management implications of this result may be minor for sculpins due to their apparently small overall impact on fry, the same concept may apply equally to other predators whose impacts on juvenile salmon appear to be much greater.

Reducing the variance in the emergence timing distribution has the effect of greatly shortening the period over which most of the fry migration occurs. The effect of this on overall mortality rates at natural spawner levels is relatively minor. Instead, the principal consequence is a dramatic shift in the spawner abundance at which the predators become swamped and mortality rates decline. While this result might offer rather limited management implications, it poses an interesting question in an evolutionary context. For predators with a Type III functional response, there is an intermediate prey density at which the prey's fitness is minimal, strictly from the standpoint of risks of predation, since the percent mortality (= probability of capture) is at a maximum. Thus, depending on the functional response of the predator, and the abundance of the prey, natural selection might favour either a concentration of spawning in time (increases prey density) or a dispersion in time (decreases density). This idea will be further examined in the next Chapter where it is considered in the context of coevolution of predator and prey.

The last three scenarios examine the relative importance of the three sculpin size classes. It is evident from
the lower panel of Figure 23 that the intermediate size class is by far the most important. Removal of this group results in a more than 50% reduction in mortality rates at all spawner abundance levels. The large sculpins have a slightly greater rate of effective search and a much greater capacity for fry, but are too rare to be of much significance. Apparently it is the large sculpins that are being swamped in the baseline scenario, since when they are removed, the percent mortality does not decline at the highest spawner abundance level.

From a management standpoint, the most important result of analyzing the model is that the mortality rates due to sculpin predation are relatively small and do not change greatly in response to changes in fry production. This suggests that prickly sculpins, despite their accelerating functional responses, are not sufficiently sensitive to changes in prey density to exert a strong regulating force on chum salmon populations. Given the large natural variability expected in these and other mortality rates (see for example Hunter's among year comparisons of survival rates at Hooknose Creek), it would seem unlikely that sculpin predation alone could be responsible for the regulation of salmon populations at relatively low levels, as discussed in Peterman (1977). Unless chum fry spend considerably more time in freshwater than is normally assumed, or in estuarine areas where alternate prey are scarce, a population level impact of prickly sculpins on chum salmon is likely to be difficult, if not impossible to detect.
VII ALTERNATIVE MODELS OF SCULPIN PREDATION

In Chapter 4, I showed that both of the models examined in this study failed in some respect to explain the results obtained in my functional response experiments. Specifically, the stochastic model failed to account for the observed variability in attack rates among individual predators, while the disc equation derived model did not predict the gorging of fry by sculpins at high prey densities. In this Chapter, I will discuss possible explanations for these deviations from model predictions, concentrating my attention on the latter result.

The stochastic model was developed specifically to test the prediction that a model based on random search and encounter could describe the predation of prickly sculpins on chum fry. As noted in Chapter 4, the inability of the model to account for the observed high degree of interindividual variation in feeding rates at a given prey density strongly contradicts this expectation. Since the predator is stationary, this suggests that the patterns of distribution and movement of the prey (which determine the pattern of their encounter with predators) deviate significantly from random. Schooling of fry may account for some of this non-randomness, but generally does not occur at night. Further, schooling itself does not guarantee a non-random encounter process, if the schools themselves are randomly distributed and move away from the stationary predator.
after a single attack takes place. On the other hand, if the fry (as schools or individuals) tend to concentrate in certain areas, independently of the distribution of sculpin predators, this might account for the high degree of variation in consumption among sculpins exposed to the same average prey density.

Alternatively, the pattern may be the result of differences among individual predators in their propensity to attack prey when they are encountered, or in their ability to capture prey once an attack has been initiated. In an experiment not reported in this study, I observed no consistent pattern of individual sculpin feeding success when five individual fish were exposed to the same prey density for four consecutive days. Individual fish did not perform consistently better or worse than their conspecifics. This suggests that such individual differences, if important, are temporary and probably reflect only very recent differences in experience. Nevertheless, they would give rise to the variability observed in my experiments.

It is possible to develop an alternative stochastic model, based on a non-random search and encounter (or attack) process, and to see whether such a model would fit my experimental results more closely. Such an exercise would provide little in the way of new insights, however. Instead, it would be more fruitful to first determine experimentally whether the potential explanations offered above are con-
sistent with observation, perhaps by directly observing the encounter/attack process. Once a possible mechanism has been observed, then the model can be revised accordingly and predictions once again compared to observation.

One of the results that is responsible for the poor fit of the stochastic model is the observation of gorging by sculpins at high prey densities. This result is also inconsistent with the Fujii model and all other disc equation based models, since they all predict a single "levelling off" of the functional response. Before turning to a discussion of possible explanations for this result, it is worth briefly reviewing the observational evidence for this unexpected predator behaviour.

1) At the highest prey densities used in 1979 and 1981 most sculpins were observed to consume far more fry than predicted from body size-maximum ration studies for other fish species (Figures 11,13). Sculpins that had fed in this manner had grossly distended stomachs and abdomens. Their stomach walls tended to be extremely thin compared to other sculpins containing fewer prey.

2) Gorging was rarely observed in experiments with low or intermediate prey densities, except in 1979 before the experiments were terminated according to the procedures described in Chapter 3. In
these early experiments (not presented in this thesis) prey and predators were allowed to concentrate in a very restricted area as the enclosure drained.

3) In laboratory feeding trials, gorging was only observed when sculpins were exposed to large numbers of fry simultaneously. When presented with fry one at a time, but on an ad libitum basis, sculpins were observed to feed only to their "normal" satiation level.

4) Laboratory observations of gorging were typically associated with increased activity by the predator. Often the sculpin would begin to chase fry about the tank, or at least alter its position of ambush frequently.

5) Both Mace (1983) and Woodsworth (1982) obtained similar results in their studies of sculpin functional responses.

In summary, these observations suggest that when sculpins are exposed to very high prey densities, their behaviour shifts from one of ceasing fry consumption at a ration level of 2-3 fry per feeding (for a 150 mm sculpin) to one of actively consuming several additional prey. In the remainder of this Chapter I present two potential explanations for this phenomenon and consider their relative likel-
ihood. The first is a passive explanation that suggests the behaviour is an inevitable result of digestive physiology. In contrast, the second explanation is a behavioural one, and proposes that the phenomenon has real adaptive significance.

7.1 Physiological Lag Model

The basic premise of this model is that there is some latency period between the ingestion of food and the resultant change in the predator's appetite. If additional prey are encountered during this period, the predator will attack and consume them before its internal homeostatic mechanisms act to inhibit further feeding. Since the rate of encounter of predators with prey is positively related to prey density, the probability of this phenomenon occurring is greater when prey are relatively abundant.

What is the evidence for the existence of a lag between ingestion and changes in appetite for fish, and what is its expected magnitude? Although a great deal of research has been conducted into the physiological control of appetite in higher vertebrates, relatively little is known about these processes in fish (Fletcher 1984). A variety of factors have been cited as having an influence on appetite in both fish and other vertebrates, including external (taste, smell, stomach fullness) and internal (plasma metabolite and hormonal levels) stimuli; the emerging consensus is that for any species, several of these factors combine to ultimately
determine the animal's rate of food intake.

For a lag of significant length (i.e., longer than a few seconds) to exist, satiation must be triggered by the animal's internal state (e.g., metabolite, hormonal levels in plasma) rather than by exterosensory inputs (e.g., stomach fullness) that will manifest themselves almost immediately. Even changes in internal state can occur rapidly, however, when the very act of ingesting food stimulates the secretion of hormones such as insulin (Murat et al. 1981). Insulin has been shown to induce suppressed feeding in higher vertebrates (Rowland and Nicolaidis 1976), although little is known concerning its role in fish feeding (Fletcher 1984). Similarly, in higher vertebrates the carbohydrates with the greatest power to suppress feeding appear to be those that metabolize most readily (Booth 1979).

On the basis of this evidence, although limited for fish, it seems unlikely that any lag that might exist between feeding and appetitive response would be very short. It is very unlikely that a period of longer than a few minutes would pass before the predator would stop feeding if its stomach were full. For even the highest prey density used in my 1981 experiments (35 prey per m²), and assuming a predator rate of effective search of 0.20m²/hr, a lag of as much as ten minutes would only result in one additional prey item being consumed, on average.
It seems unlikely, therefore, that sculpin gorging is simply a result of digestive physiology. Even if a lag exists, and is relatively long, the effect of this process on the functional response would not be to give rise to a threshold effect, as is suggested by my experimental results (and those of others). As prey density increases, so the frequency of sculpin encounters with prey will increase. With a fixed lag time, this should give rise to a functional response that increases linearly at high prey densities, rather than decelerating towards an asymptote and then accelerating again. The only circumstance that might give rise to the observed pattern would be if the rate of encounter actually increases much more rapidly than the prey density. As argued by Taylor (1979, 1981), this situation is unlikely to arise given selective pressures upon the prey population to minimize their losses due to predation. In fact, Taylor's arguments would suggest that, if anything, encounter rates will increase in less than direct proportion to increases in prey density, thus giving rise to a functional response that rises less than linearly at high prey densities.

7.2 Optimal Foraging Model

If gorging is not an involuntary result of digestive physiology, then the sculpins must be actively choosing to increase their intake at higher prey densities. In the previous Chapter, I noted that prey may gain an advantage by
aggregating in time (i.e., reducing the variance of their emergence timing distribution), thereby "swamping" their predators. Similar arguments have been advanced as a basis for the presence of aggregations in space such as schools of fish and herds of ungulates (e.g., Hamilton 1971). Perhaps gorging is simply a counter-adaptation whereby the predator reduces the negative consequences to its own fitness of infrequent periods of super-abundant prey.

While this explanation may seem quite reasonable, it is difficult to see why a threshold effect would be observed if the gorging is solely a consequence of the predator increasing its capacity for prey to minimize the impacts of prey patchiness in time. Why not simply consume as many prey as possible, whenever they are available? To find an explanation for the threshold, it is necessary to examine the phenomenon from an optimal foraging perspective.

In developing the theory of optimal foraging, several authors have noted that the foraging behaviour of an animal, including the amount of time it spends foraging, is expected to be a consequence of trading off the risks of foraging against its benefits (Schoener 1971, Rosenzweig 1974, Covich 1976). The most commonly cited risk faced by foragers is that of predation on the forager itself. Several studies have shown experimentally that in fact the behaviour of a forager is influenced by the risk of predation (Stein 1977, Milinski and Heller 1978, Caraco et al. 1980, Sih 1980,
1982, Kotler 1984). Since the benefits of foraging (but typically not the risks) will clearly depend on the density of prey it is quite possible that a forager's behaviour will change as prey density changes. Specifically, a relatively risky foraging activity may become optimal if the prey are sufficiently abundant that the potential rewards justify the risk.

Abrams (1982) has examined theoretically the influence of these optimal foraging concepts on functional response models. Using very simple models of birth (benefit) and death (risk) rates as a function of time spent foraging and prey density (birth rate only), he has shown that functional response forms can be obtained that are more complex than those described by Holling's four response types. In particular, he has demonstrated that a response form with a decelerating phase followed by an accelerating phase (typical of the gorging response) is possible.

To show that optimal foraging theory offers an explanation for the gorging behaviour observed in this study, it is necessary to develop a simple model of sculpin foraging. The model is used to predict the amount of time spent foraging by sculpins and the amount of prey consumed during this time. By applying the model over a range of prey densities, the resulting functional response can be described.

My observations indicate that prickly sculpins are typically ambush predators. Such a foraging strategy is
presumably effective at minimizing the risk of predation. On the other hand, my laboratory observations of gorging also suggest that sculpins change their behaviour to a pursuit "mode" when confronted with very high densities of prey. This type of behaviour presumably greatly increases the risk of predation. The model thus divides the total time available for feeding into three classes: (1) not foraging (digestive pause); (2) ambush foraging; and (3) pursuit foraging.

Optimal foraging models require that some metric of net benefit be described and quantified, so that the choice of foraging strategy can be based on its maximization. The model I present here is similar to those of Abrams (1982) in that it assumes that gross benefits are determined by the prey density and time spent foraging, and that risks are influenced by time spent foraging. It differs from Abrams models, however, in that sculpin hunger is explicitly accounted for as a factor that affects the gross benefit function. Net benefit is simply the difference between gross benefits and risks. The model works by calculating, for any prey density and state of sculpin hunger, the net benefit of being in each of the three foraging classes
The sculpin is assumed to select the state that offers the greatest net benefit.

To examine the influence of this foraging model on the functional response, I embed this decision rule into a dynamic model that simulates the feeding of sculpins during a series of short time intervals over an extended period of time (e.g., a 15 hour experimental period). In each time step, the foraging state is chosen, and the resulting number of prey consumed is calculated (from $a_i \cdot N_0$). This process is repeated for the entire period, and for a range of prey densities, to yield a prediction of total prey consumption as a function of prey density.

The model makes two critical assumptions. First, the risks of predation increase as the sculpin shifts from digestive pause to ambush to pursuit mode. Second, the rate of effective search of sculpins is assumed to be greater in pursuit mode than for ambush mode. The first of these is
easily justified: clearly a sculpin that is both moving and in the open is exposed to greater risk than one that is stationary. The second is less obvious, although it would be equally difficult to dismiss as to justify. While a pursuit predator will have a greater reactive distance, its capture success for highly mobile prey may be greatly reduced. Suffice it to say that unless this assumption is true, the sculpin will never elect to pursue its prey.

The form of the functional response generated by this model depends largely on the assumed relationship between the state of fullness of the sculpin's gut and the benefit of further feeding ($f(h)$). If a monotonic relationship is assumed, the functional response will not exhibit the additional acceleration phase due to gorging. Instead it will rise monotonically to an asymptote defined by the maximum capacity of the sculpin's gut. As the prey density rises, the sculpin will spend more and more of its time in pursuit mode, but the change will be gradual. This is because the prey density at which the net benefit of pursuit exceeds that of ambush is influenced by sculpin stomach fullness:

$$\text{if } N_0 > \frac{R_3 - R_2}{f(h) \cdot (a_3 - a_2)} \text{ then choose state 3.}$$

At any prey density sufficient to initiate pursuit foraging, the sculpin will consume prey, thereby increasing its state of fullness and reducing the relative benefit of pursuit
versus ambush. With a monotonic "hunger" function, the amount of feeding that takes place in pursuit mode will increase monotonically with prey density.

To obtain a functional response that includes the gorging phenomenon observed in this study, it is necessary to assume that a more complex relationship exists. Specifically, \( f(h) \) must exhibit two levels separated by a rapid decline from the higher to the lower. At first this might seem like an ad hoc "model" of appetite, but there are energetic considerations that support such a pattern. The lower level of stomach fullness may indicate the consumption that is needed to meet maintenance (and thus survival) requirements. Fish that have not reached this state of fullness may be prepared to take far greater risks to obtain more food than those that have. Any extra feeding would be less critical but nevertheless beneficial, serving to offer additional scope for growth.

This model is consistent with the coevolutionary hypothesis that gorging has evolved in response to a patchy temporal distribution of prey. It complements this perspective by offering an equally adaptive explanation for the existence of a threshold response, whereby the behaviour is only exhibited at high prey densities. Perhaps more significantly, it offers a plausible theoretical basis for a functional response model that accommodates a more complex form than allowed by the traditional models.
To suggest that my functional response data offer more than circumstantial evidence in support of this model would be unreasonable. In fact, a definitive test of the model may prove difficult to conceive, let alone design. Manipulations of the risk of predation are unlikely to be useful, since the phenomenon was observed in the lab. If sculpins are trading off benefits against risks, the risks of being in a particular state are apparently predetermined and fixed rather than dependent on a perception of current conditions. On the other hand, manipulations of the benefit function could be conducted, perhaps by altering the quality of the prey (e.g., size, species). This would be insightful only if the sculpins use some other metric in addition to prey density to determine benefits. Further functional response experiments conducted at intermediate and high densities could be used to better establish the presence of the threshold, but would not help to discriminate among alternative models.

A more promising approach to testing the hypothesis might be to observe sculpin behaviour when subjected to contrived situations. For example, one could expose sculpins to a variety of prey densities, without actually allowing them to feed, perhaps by using transparent partitions in a laboratory aquarium. The optimal forager model would predict that the sculpins would alter their behaviour (i.e., begin to move around in pursuit of prey) when prey densities were perceived to exceed a threshold level. The physiological
model would not predict this response.

Whether or not the optimal foraging model is a valid explanation for sculpin gorging, the very existence of this behaviour has theoretical implications of relevance to the central question posed by this thesis: do prickly sculpin impose significant predation mortality on juvenile chum salmon? In the previous Chapter, I ignored gorging in developing estimates of the impact of sculpins on chum fry. This omission will give rise to incorrect estimates of overall prey mortality if two conditions are met. First, prey densities must have exceeded the level at which gorging would be expected to occur. In most scenarios presented for Rosewall Creek this was the case only for very high spawner abundances. Second, the period of digestive pause between successive meals must not increase in direct proportion to meal size; otherwise the sculpins will simply consume more fry than in the absence of gorging, but less often, with no net effect on overall prey consumption. Actually, the fact that prey densities vary through time complicates this issue, but the essential point remains the same: the relationship between meal size and digestive pause must be known to accurately assess the impact of gorging on prey populations.
VIII CONCLUSIONS

In discussing my experimental results in earlier chapters, I concentrated on the agreement or lack thereof between the predictions stated at the end of Chapter 2 and my own observations. To summarize these results:

1. The functional response appeared to be sigmoid (Type III) in two of the three years, although the results are not entirely unambiguous.

2. Rates of effective search were observed to be far lower than the expected range of 1.0 to 8.0 m²/hr.

3. Large (150 mm) sculpins showed evidence of a maximum ration of between 2.5 and 4.0 fry per feeding, although gorging was observed at high prey densities.

4. The predator-prey interaction does not appear to be a purely random process.

5. Alternate prey did affect apparent search rates but not the maximum ration of sculpins feeding on chum fry.

6. Both search rates and maximum ration increased with increasing predator size.

7. Prey size did not appear to affect predation rates at least for large sculpins.
Possible reasons for the deviation of individual results from expectation have been the subject of much earlier discussion; it is not my purpose to reiterate these discussions here. Instead, I will consider my results in the aggregate, and with reference to the central question posed by this thesis: in predator-prey systems involving fish feeding on other fish, what influence does the predator have on the population dynamics of its prey?

First, my results indicate that for the particular interaction I examined, the abundance of the predator and the degree of spatial and temporal overlap in the distributions of predator and prey are more important than the functional response itself in determining the impact of predation on the prey population. I would argue that this conclusion is generally true of predators on migratory fish, unless their individual capacities for prey are very large, as may be the case for some avian predators of juvenile salmon. For prickly sculpins the impact appears to be minor unless the fry remain for some time in areas of sculpin abundance. It is not possible to generalize from this study what the impacts of other natural predators might be, but I would recommend that assessments of other predators focus first on their abundance and distribution, and subsequently on their functional response. The former is arguably easier to measure, at least approximately, and may expedite the process of narrowing down the rather long list of candidates for more detailed study.
Second, and perhaps equally important is the conclusion that the abundance of alternate prey may have almost as much influence as the abundance of the principal prey population itself. Again, this is probably a result of general significance, as many fish species are touted as generalist feeders (e.g., Larkin 1978). Changes in the abundance of alternate prey, possibly mediated by forces unrelated to the predator and principal prey populations, may nevertheless have a profound impact on the interaction of primary interest. Not only will reductions in alternate prey stimulate dramatic shifts in predation to the principal prey population, but abundant alternate prey may support a relatively large predator population even if the principal prey is only temporarily present.

Further, these two conclusions are connected, since it is likely that a predator population sufficiently large to impose substantial impacts on a migratory prey population will only exist where alternate prey are abundant. The alternate prey themselves may vary considerably in abundance over time, as appeared to be the case for the invertebrates consumed by sculpins in the Fraser estuary. This implies that the effect of predation on the principal prey will depend critically on the timing of their presence in areas of predator abundance, relative to the temporal pattern of alternate prey abundance.

Third, the functional response itself points to an
additional, general conclusion. Increases in fry abundance, perhaps due to artificial enhancement efforts, are unlikely to benefit the fry population due to predator swamping, unless such increases are very great. The low rates of effective search by the predator combined with the presence of a Type III response are responsible for this conclusion. In fresh waters at least the overall impact of prickly sculpins on chum fry appears to be small, however, so enhancement efforts should not be expected to be measurably offset by increases in sculpin predation. On the other hand, for a more abundant or larger predator, this might not be the case.

Finally, this study has shown that existing simple models of the functional response do not adequately explain the observed pattern of predation by prickly sculpins on chum fry. Since both predation based on random, or deterministic processes and predator gorging are phenomena that are by no means unique to prickly sculpins, I would argue that a more general predation model is needed than that offered by the current generation of disc equation based models. These latter models may have received a mark of generality that is not entirely justified, at least for vertebrate predators. To achieve this generality, it is essential that alternative models such as those presented in Chapter 7 be developed and tested empirically, in much the same fashion as done in this study for the stochastic model. Both science and management demand this progress.
REFERENCES


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