INFORMATION QUALITY AND UNCERTAINTY IN RESOURCE ALLOCATION DECISIONS

by

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ABSTRACT

As demands on a finite supply of natural resources have intensified, decision makers have found it increasingly difficult to maximize the benefits of resource developments while ensuring that the biophysical bases of resource uses are maintained. These problems are accentuated when decision makers cannot predict the outcomes of resource allocations because of a lack of information regarding existing resource uses. This thesis therefore examines the influence of data quality and conditions of uncertainty on decision makers' ability to maximize the benefits and minimize the negative impacts of resource allocations.

Decisions can be made under conditions of certainty. risk or uncertainty, with each condition reflecting the relative predictability of decision outcomes. Uncertainty can only be reduced by gathering "functional" information, which specifies the interrelationship between elements of systems potentially affected by a decision. Subjective attempts by decision makers to reduce uncertainty may lead to biased assessments of decision outcomes.

Discharge and spawning habitat data for selected Vancouver Island salmon spawning streams was found to be completely "descriptive" in quality; this data, which merely outlines discharge and spawning habitat conditions as unrelated entities, does not allow resource decision makers to predict possible effects of small hydro developments on downstream spawning habitats. Thus, streamflow allocations for small hydro plants on these streams would be made under conditions of uncertainty. Decision makers will not be able to maximize the benefits of small hydro developments while minimizing negative impacts on spawning habitats.

To facilitate effective resource allocations, decision makers should be made aware that 1) information quality and uncertainty are linked, and 2) subjective methods of uncertainty reduction will lead to unforeseen or undesirable outcomes to resource decisions. Finally, the advantages of anticipating and collecting functional-quality data in advance of a resource decision process are stressed.

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CHAPTER 1

UNCERTAINTY IN RESOURCE ALLOCATION DECISION MAKING: RATIONALE AND RESEARCH STRUCTURE

1.1 Introduction

Over the past half century, a growing population and a consumer-oriented economy have contributed to increasing demands for natural resources and a collateral increase in the complexity of resource allocation decision making. As the number of resource users ~~has~~ have grown and demands for the finite resource supply have intensified, it has become more difficult for decision makers to garner the benefits of resource developments while ensuring the biophysical foundations of existing and future resource uses are maintained. Allocative decision making under these conditions can be complicated; the problems are accentuated when information relevant to the decision situation is incomplete or lacking and when there is a need for an immediate decision. In these instances, an allocative decision may be made under conditions of uncertainty where the decision maker is unable to specify the possible effects of that decision on the resource base.

Decision theory suggests that conditions of uncertainty and the related states of risk and certainty arise from the decision maker's ability to predict outcomes of possible courses of action (March and Simon, 1959). Under conditions of certainty, where the types and magnitudes of outcomes can be accurately predicted, an allocation decision can be made which maximizes benefits while minimizing or avoiding environmental degradation and resource use conflicts. Under conditions of risk the specific outcome cannot be determined; however, the decision maker can determine the relative likelihood of possible decision outcomes. Even though a specific outcome cannot be guaranteed, a decision can nonetheless be made based on the expectation that the most probable consequences will indeed occur. Finally, under conditions of uncertainty where neither the specific outcomes nor the probabilities of their occurrence can be accurately determined, an allocation decision may result in unanticipated (and often undesireable) effects including resource use conflicts and negative impacts on ecological processes and resource uses. Thus, uncertainty in the decision process may lead to an ineffective (in terms of achieving desired outcomes) resource allocation. To facilitate effective decision making, it is therefore necessary to reduce or convert uncertainty to a condition of risk or certainty.

The ability to predict or assign probabilities to outcomes can be characterized as a spectrum ranging from a condition of ignorance, where nothing is known of the possible outcomes, to a condition of certainty wherein a specific outcome can be determined for each alternative course of action. Between these extremes are situations where the decision maker may or may not be able to assign probabilities to possible outcomes of alternative decisions. A condition of risk exists between the point at which the decision maker can assign probabilities of outcomes up to, but not including, the point where he is completely certain of one specific outcome as a result of a decision. A condition of uncertainty, on the other hand, occupies that portion of the continuum from complete ignorance up to but excluding the point at which a condition of risk begins. As Archer (1964) suggests, "Short of risk conditions, exists uncertainty."

Decision theory suggests that the ability to assign probabilities to possible outcomes of a decision is determined by the decision maker's understanding of the systems or environments potentially affected by the decision (March and Simon, 1959; Miller and Starr, 1967; Bridge and Dodds, 1975). Essentially, the more information available to the decision maker concerning the internal processes of a system, the greater a decision maker's ability to predict the effects on that system of actions arising from a decision. This predictive power in turn allows the decision maker to assign probabilities to these outcomes.

Information concerning the internal processes of a system can be characterized as a spectrum ranging from purely descriptive or non-functional information to a complete body of functional knowledge. As the term suggests, descriptive information merely describes elements within a system while offering no explanation of linkages or relationships between these elements. Examples of descriptive information in an ecological context might include distribution of species, size and types of populations, or volumes and quality of water bodies. On the other hand, functional knowledge goes beyond a description of static elements within a system to specify the causal relationships between these elements, or in other words, a system's internal processes. Examples of functional information, again in an ecological context, might include an understanding of nutrient cycling or the pattern of energy flows within a defined aquatic or terrestrial ecosystem.

Effective resource allocations can only occur when decision makers understand the effects of alternate allocation strategies on existing or future resource uses. According to decision theory, such effects can only be understood if decision makers possess functional information which specifies the systemic operation and mutual dependence of elements which form the bases of the resource uses in question. Where this information is available, the possible effects of allocation strategies can be identified, evaluated, and compared, thus ensuring that the selected allocation strategy will derive the maximum benefits while preserving (to the greatest degree possible) the systemic bases of existing and future resource uses.

The problem with resource decisions is that the information available to the decision maker may be predominantly descriptive rather than functional in nature. Since a finite amount of time and financial resources are allotted to the decision maker during the decision process, and because information-gathering can be very costly in terms of time and money, it thus may not be possible to acquire sufficient functional information in advance of a decision (Braybrooke and Lindblom, 1963). In these circumstances, the decision maker may not be able to determine the relationship between alternative allocation strategies and possible effects on ecosystem processes which form the bases of resource uses.

The intent of this thesis is to examine the nature of uncertainty in decision making and ascertain whether (as decision theory suggests) a lack of functional information will lead to ineffective decisions. These observations are then applied to a hypothetical case of resource allocation decision making: the possible development of small scale hydroelectric (SSH)[1] generating potential on Vancouver Island salmon spawning streams.

The hypothetical SSH proposal is chosen for the case study for two reasons: 1) flow alterations arising from SSH development on salmonid-producing streams could have significant overall effects on salmonid spawning habitats, thus providing the basis for considerable conflict between developers, government agencies, and public interest groups; 2) information concerning the relationship between discharge levels and spawning habitat conditions may be lacking; thus, decision makers might be unable to predict the potential changes in spawning habitat quantity and quality. The protection of instream salmonid habitats has been accorded a high profile in British Columbia, with the social value of the salmon resource deemed sufficiently high to warrant a great deal of effort and expense to preserve its viability. Activities perceived as being deleterious to salmonid habitats have led to intense, emotional conflicts between government agencies, public interest groups, and development interests. To date, hydroelectric developments on Vancouver Island rivers have avoided such conflicts, primarily because most were situated on rivers without significant instream salmonid habitats. That situation could change with widespread SSH

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[1] Small scale hydroelectric (SSH) facilities have been defined as those with installed generating capacities of 20 MW or less (British Columbia Hydro and Power Authority,1982); however, a study undertaken by Crippen Consultants (1980) chose to distinguish facilities with installed generating capacities of 2MW or less as "micro-hydro" installations. For the purposes of this study, SSH facilities will hereafter refer to those hydro plants with installed generating capacities between 2 and 20 MW.

SSH development on the Island since a number of potential SSH sites are located on rivers which are extensively used by spawning salmon. While a single SSH facility does not have the inherent capability to produce massive changes in watershed characteristics as does a large hydroelectric dam, the potential exists for spatial and temporal changes to flow regimes as a result of a SSH facility's operations. These flow alterations, if multiplied by the number of SSH facilities built on salmonid-producing rivers, can result in substantial changes in the quantity and quality of spawning habitats.

Changes to streamflow characteristics have been chosen to illustrate how SSH facilities and operations may affect instream salmonid habitats provided by several Vancouver Island rivers. The rapid and pronounced alterations in stream depth and velocity arising from the generation of "peaking power" at SSH facilities may negatively affect the spawning success of returning salmonids, thereby reducing the subsequent number of hatching salmon (Hamilton, 1978, Loar and Sale, 1981). Conditions of uncertainty will exist if a decision maker cannot determine cause-and-effect relationships between changes in flow regimes occuring as a result of SSH development and the impacts on salmonid spawning. Thus, a proposal for SSH development highlights the need for a sufficiently complete body of information regarding the effects of SSH operations in order to reduce or eliminate potential conditions of uncertainty in the decision process.

This research will investigate the following argument:

> If available information concerning the effects of SSH facilities and operations on salmonid spawning habitats is primarily non-functional in nature, then an allocation of streamflow for SSH peaking power generation will result in unanticipated or undesireable effects on spawning habitats.

1.2 Research Structure and Procedure

Chapter 2 reviews the theortetical background to decision making under conditions of certainty, risk, and uncertainty. Distinctions between conditions of certainty, risk, and uncertainty are reviewed in terms of the decision maker's ability to assign objective probabilities to possible outcomes or effects of a decision. The role of information in determining outcome probabilities is then discussed and linkages between the availability of functional information and states of certainty, risk, and uncertainty are outlined. Some of the possible effects of decision making under conditions of uncertainty are then analyzed. The intent of this chapter is to demonstrate why decision making under conditions of uncertainty is unacceptable for resource allocations.

Chapter 3 provides the background to a hypothetical proposal for small scale hydroelectric (SSH) development on a number of Vancouver Island salmon spawning streams. Vancouver Island's current peaking requirements are reviewed and the role of SSH facilities in meeting future peak load requirements is described. Spatial and temporal modifications in streamflow below SSH peaking facilities are reviewed. Discharge and water depth parameters preferred by spawning salmon are outlined in order to highlight the possible effects of streamflow modifications on the quantity and quality of spawning habitats below SSH peaking facilities.

Chapter 4 examines the existing discharge and spawning habitat information for selected Vancouver Island rivers to a) identify the quality of available data and b) determine whether the information quality will foster conditions of uncertainty in SSH decision situation. The quality of available information is estimated on the basis of the degree to which that data specifies a causal relationship between discharge and spawning habitat conditions in each river. Then, the linkage between these appraised information qualities and decision makers' ability to estimate or predict the effects of modified flows on spawning habitats is outlined. On the basis of the previous discussion, an assessment is made of the conditions of uncertainty, risk or certainty which would likely prevail in decisions to develop SSH peaking power facilities on Vancouver Island salmon spawning streams.

Finally, in Chapter 5, the influences of descriptive and functional information in promoting or reducing uncertainty in resource allocation decision making is reviewed with reference to the research argument. Implications for resource allocation decision making are discussed and conclusions are forwarded.

CHAPTER 2

QUALITY OF INFORMATION AND UNCERTAINTY IN DECISION SITUATIONS.

2.1 The Nature of Decision Making

The decision process is generally characterized as a series of distinct phases or steps culminating in a choice between two or more courses of action (Richards and Greenlaw, 1972). As part of this process, decision making has been defined as "...in a broad sense, the selection of alternative courses of human action..." (Kates, 1962, p.12) or more specifically, the selection of "...an expectedly most favorable alternative..." (Sutherland, 1977, p.4). Two models of decision making have been advanced. The model of "economic man" views the decision maker as a purely rational being making optimal choices in a highly specified and clearly defined environment (Luce and Raiffa, 1957; Machol, 1960; Gordon et al, 1975). When confronted with a problem requiring a decision, economic man is presumed by these normative theorists to:

1) Clearly define the decision criteria.
2) Be knowledgeable of all relevant alternatives.
3) Be aware of all possible consequences of each alternative.
4) Evaluate the consequences against the decision criteria.
5) Select the alternative which is most preferred in terms of satisfying decision criteria.

(Cyert et al, 1959)

Assuming that major parameters of the decision situation can be readily identified, quantified and ranked, normative theorists suggest that alternate courses of action can be rationally evaluated within the decision process and a course of action objectively selected which most efficiently achieves the desired goals or objectives (Gordon et al, 1975). Critics of the normative approach point out that decisions are not usually made in an environment where all relevant alternative courses of action or all possible consequences of these alternatives are known by the decision maker (Simon, 1957;1959). Since the full range of variables influencing or affected by decisions can only be quantified where the decision environment is relatively simple and a great deal of information about this environment is available (Richards and Greenlaw, 1972), the normative model of economic man has come to be seen as a idealistic model of decision making rather than a description of actual processes of choice.

Simon (1957) attacked several basic tenets of the economic man model, stating that in actual decision situations it was not feasible to search for every alternative, that decision criteria cannot always be objectively stated, that human beings have a limited capacity for understanding complex decision situations, and that decisions are not necessarily made in an environment of certainty where all possible courses of action and their consequences are known. His "administrative-man" model, which is intended to reflect actual decision making behavior, therefore proposes that a decision maker will:

1) Recognize only a limited number of criteria.
2) Propose only a limited number of alternatives.
3) Be aware of only a few of each alternative's consequences.
4) Formulate a simplified and limited model of the real situation.
5) Select the alternative which presents a satisfactory solution.

(Robbins, 1980).

In this model, alternatives are not fixed and known, goals may be vague and inconsistent, and information concerning the decision situation may be incomplete or lacking. During the decision process, the decision maker will typically attempt to reduce the complexity of the decision situation by constructing a simplified model of the factors or variables involved in the decision, thereby limiting the variables requiring consideration and allowing a decision to be made within the limitations of the intellect or personal knowledge of the decision maker (Simon, 1959). In these situations, the values and experience of the decision maker tend to strongly influence the identification and evaluation of alternative courses of action. Decisions in these cases would therefore not represent rational or objective choices based on a complete understanding of the decision's consequences, but rather choices reflecting subjective estimates or biases concerning the expected outcomes of these decisions (Scott, 1967).

The administrative-man model postulated by Simon (1957, 1959) suggests that decision processes are in reality somewhat subjective exercises in which choices are made on the basis of limited or incomplete information concerning either the alternative courses of action or the consequences of these actions. According to this analysis, decision makers are either unwilling or unable to comprehend the complexity of variables inherent in a decision situation, and as a result, decision situations are simplified to conform to the personal experiences of the decision makers. Similar views are shared by theorists concerned with decision making in situations where the decision maker possesses variable amounts of information regarding the possible outcomes of a decision (Scott, 1967; White, 1969; Mack, 1971; Bridge and Dodd, 1975). Bridge and Dodd suggest that a decision maker will only rarely be able to make a decision under conditions of certainty where all outcomes of alternative courses of action can be specified. Instead, a decision maker more commonly must choose under conditions of risk, where only the relative likelihood of various decision outcomes can be determined, or under conditions of uncertainty where little or nothing is known of either the possible consequences of a decision or the probabilities of these outcomes' occurrence. In common with the model of administrative man, the decision maker facing conditions of uncertainty may attempt to simplify the decision situation or to use subjective estimates of the outcomes of possible courses of action. The result may be an overly restricted framework in which to assess possible courses of action or the intrusion of subjective biases into the decision process (Mack, 1971).

2.2 Decision Making Under Conditions of Uncertainty

2.2.1 Certainty, Risk and Uncertainty Conditions.

In light of Simon's (1957, 1959) formulation of actual decision processes, a great deal of attention has focussed on the manner in which a decision maker's knowledge of the possible consequences of alternative strategies can affect the decision process (Wilson and Alexis, 1964; Richards and Greenlaw, 1972). March and Simon (1959) propose that in any decision situation, one of three states of knowledge exist with regard to the relationship between a decision and its possible outcomes:

1) Certainty: The complete set of environmental conditions which affect or are affected by a decision are known by the decision maker.

2) Risk: Accurate knowledge exists about the probability distribution of possible outcomes of each alternative courses of action.

3) Uncertainty: The consequences of each choice cannot be identified or defined within a probabilistic framework (March and Simon, 1959).

The implication of a condition of certainty in a decision situation is that the decision maker is fully aware of the consequences of each possible choice; therefore each alternative course of action has a single known outcome. A decision in this situation is relatively straightforward. The decision maker simply chooses a course of action which will result in the most desirable outcome. Unfortunately for the decision maker, conditions of certainty are rarely encountered in actual decision situations, and thus certainty represents an ideal rather than a typical state in which decisions are made (Wilson and Alexis, 1964; Robbins, 1980; Anderson, 1982).

More commonly encountered are conditions of risk or uncertainty in decision situations. Risk conditions are said to exist when the decision maker is able to estimate the probabilities of decision outcomes (Robbins, 1980). Although the outcome of a choice is not certain in these circumstances, the decision maker may sufficiently understand the relationships between alternative courses of action and the possible outcomes of these strategies that he is able to determine the relative frequencies of these outcomes. Thus, while a specific outcome cannot necessarily be predicted, a decision can nonetheless be made based on the expectations that the most probable consequences will occur (Miller and Starr, 1967). On the other hand, uncertainty in a decision situation implies that the decision maker cannot determine the outcomes of various decision alternatives or the relative frequencies of these outcomes' occurrence.[2] Conditions of uncertainty therefore exist when the possible consequences of a choice are wholly or partly unknown by the decision maker, or when the decision maker is unable to determine the likelihood of possible outcomes' occurrence. Under conditions of uncertainty, there are no objective guidelines to indicate which outcome of a decision will occur; thus, a decision may result in any one of a number of consequences, some of which may not have been anticipated by the decision maker.

A growing interest in the mathematical or statistical bases of decisions has led to conceptualizations of certainty, risk, and uncertainty within a probabilistic framework. Probabilistic views of certainty, risk, and uncertainty conditions in decision making define these conditions in terms of a decision maker's ability to determine the relative frequencies or probabilities of occurrence for possible outcomes of a selected course of action (Figure 2-1). Accordingly, the decision maker's

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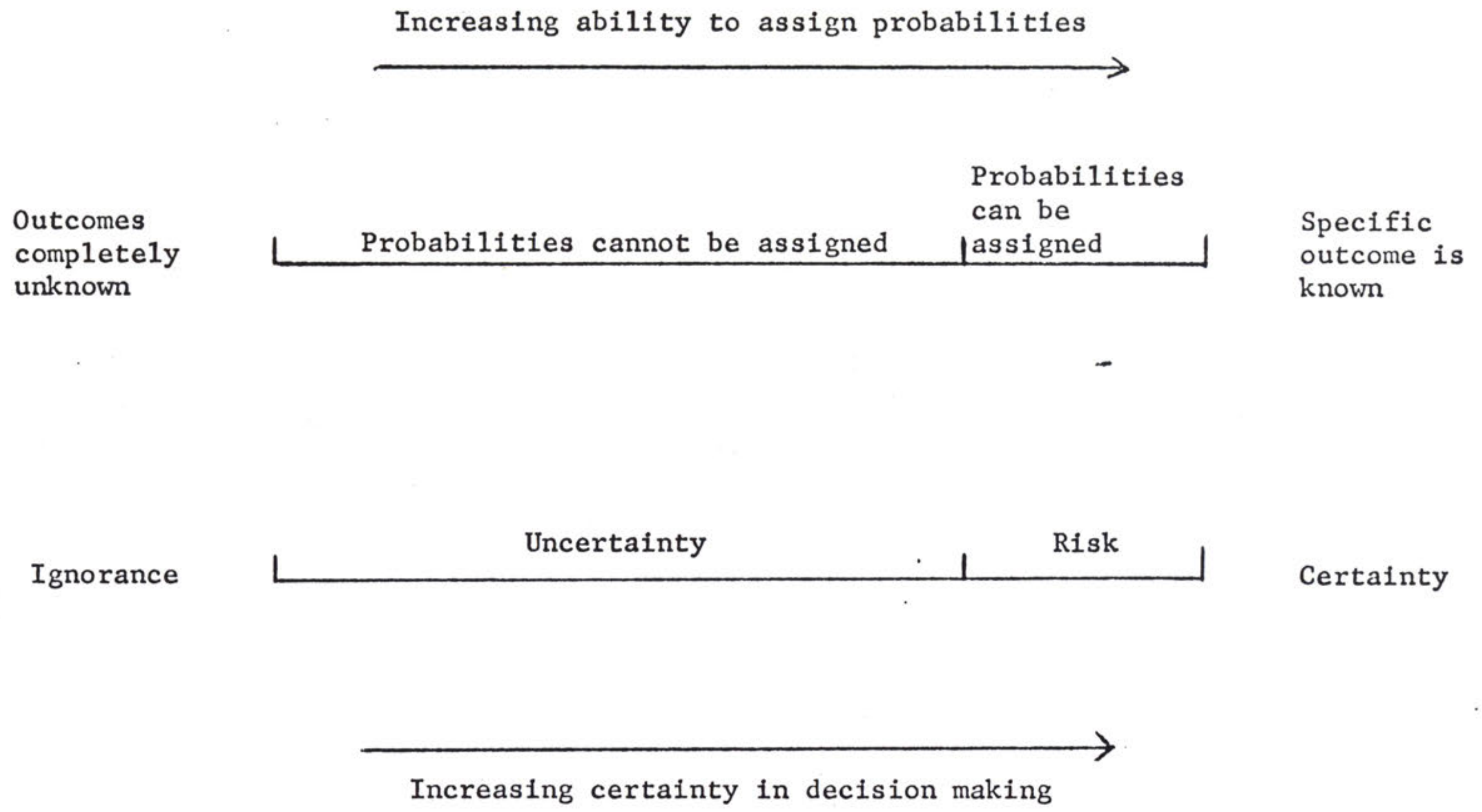
[2] The concept of uncertainty in decision making can be linked to other aspects of the decision situation; for example, Ebert and Mitchell (1975) identify uncertainty in the identification of relevant decision variables and uncertainty concerning the relationship between relevant variables as factors detracting from the degree of control that can be exercised by the decision maker in the decision process. For the purpose of this discussion, however, "uncertainty" will refer to a decision maker's inability to objectively determine the relative likelihood of outcomes or consequences resulting from alternative courses of action.



(Adapted from Willis and Chervany, 1974)

FIGURE 2-1. ABILITY OF DECISION MAKERS TO ASSIGN PROBABILITIES TO DECISION OUTCOMES AND CONDITIONS OF CERTAINTY, RISK AND UNCERTAINTY IN DECISION SITUATIONS.

ability to determine the probabilities of decision outcomes can be depicted as a spectrum ranging from the point at which the decision maker is completely incapable of predicting a decision's consequences to the opposite extreme where the decision maker is capable of predicting the exact outcome of a decision (Willis and Chervany, 1974). In decision situations where the decision maker is unable to determine either the full range of outcomes or the relative frequencies of their occurrence, the assignment of probability values to possible outcomes is theoretically meaningless (Dyckman _et_ _al_, 1969); this condition is considered as equivalent to a state of ignorance in a decision situation (White, 1969). The opposite end of the spectrum reflects those situations in which a decision maker is able to specify the single, determinate outcome of a decision. In the more familiar terminology of horse race betting, the decision maker can in this case state with assurance that one specific horse in a race will win, and that no other horse has even the slightest chance of winning. His bet (or decision) is therefore based on this specific, guaranteed outcome. In a case where the decision maker can objectively determine that there will be only one outcome associated with each strategy, he can be completely sure that a selected course of action will result in a specific and known outcome; this condition can be seen as equivalent to that of certainty in a decision situation (White, 1969).

Between these extremes are ranges on the spectrum representing the decision maker's ability or inability to determine the relative frequencies of decision outcomes. According to statistical decision theory, a condition equivalent to one of risk exists when the decision maker can determine the probability distribution for the possible outcomes of a decision (Menges, 1973; Willis and Chervany, 1974; Anderson, 1982). Again using the betting analogy, the decision maker operating under conditions of risk knows that there are only six horses in the race, and also knows the odds for each horse running the race. His bet thus lies with the horse which he knows has the greatest chance of winning, even though there is a possibility that another horse may in fact win the race. Although the outcome of a decision cannot be deterministically predicted, the fact that the probabilities of outcomes can be determined means that a choice can be made based on the expectation that the outcome with the highest probability will indeed result from a selected course of action. As indicated in Figure 2-1, the ability of the decision maker to assign probabilities to possible outcomes extends up to, but does not include, the point at which a specific outcome can be determined. The ability to assign probability values to possible decision outcomes can thus be seen as equivalent to a condition of risk in a decision situation.

A condition of uncertainty is assumed by statistical decision theory to exist when a decision maker is unable to determine either the possible outcomes of alternative courses of action or the probabilities of these outcomes' occurrence (Richards and Greenlaw, 1972; Bridge and Dodds, 1975; Anderson, 1982). Like conditions of risk, uncertainty exists in a decision situation when more than one outcome can occur as a result of a chosen course of action. Unlike either conditions of risk or certainty, however, a decision maker operating under conditions of uncertainty may not be able to identify the full range of possible consequences of a decision or cannot determine the relative frequencies with which these outcomes could be expected to occur. Using the betting analogy once again, a decision maker betting on a horse race and operating under conditions of uncertainty does not know how many or which horses are in the race, and cannot determine the odds of any horse winning. His bet could, therefore, by chance, be placed on the subsequent winning horse, but it is also very likely his bet will land on a horse which will not win the race. Under these conditions, statistical decision theory indicates that a decision maker cannot be sure of which outcome will occur or even which outcome is most likely to occur as a result of a decision; thus, a decision maker has no objective basis to determine whether a selected course of action will result in desirable, undesirable, or even unanticipated consequences (Miller and Starr, 1967;

Aitchison, 1970; Menges, 1973). As illustrated in Figure 2-1, the inability of the decision maker to determine probabilities of possible outcomes extends from a state of ignorance up to a point where the relative frequencies of outcomes can be assigned. This inability of the decision maker to determine probabilities of outcomes can be seen as equivalent to conditions of uncertainty in a decision situation.

In sum, the ability of a decision maker to specify a single determinate outcome or to assign probabilities to a finite range of possible outcomes, or his inability to determine either the range of possible outcomes or their probabilities of occurrence, can be seen as equivalent to conditions of certainty, risk and uncertainty respectively. Statistical decision theory demonstrates that a condition of certainty, risk, and uncertainty observed in a decision situation ultimately depends on the ability of the decision maker to objectively predict the consequences of a decision. Where this objective predictability is absent or replaced with subjectively-based prediction of decision outcomes, so too will uncertainty be present in a decision situation.

2.2.2 Effects of Uncertainty on the Decision Process and its Outcomes.

There is a general consensus among decision theorists that conditions of uncertainty, if not reduced to conditions of risk or certainty, can detrimentally affect the objective assessment of alternatives within a decision process and may enhance the possibility of unanticipated or negative outcomes as a result of a decision. It should be pointed out, however, that a state of uncertainty does not by itself affect the decision process or the results of a decision; rather it is the responses of the decision maker upon perceiving uncertainty that links conditions of uncertainty with undesirable effects on decision processes or decision outcomes (Downey, 1974). Thus, in order to understand the effects of uncertainty, it is first necessary to outline the possible responses of the decision maker which allow conditions of uncertainty to persist as a feature of a decision situation.[3]

In her discussion of uncertainty in administrative environments, Mack (1971) suggests that upon perceiving the existence of uncertainty in a decision situation, a decision maker may respond in one of two ways: 1) he may suppress the fact of uncertainty, or 2) proceed in attempts to cope with uncertainty. She goes on to suggest that a decision maker may attempt to cope with uncertainty by restricting the type or number of variables which will

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[3] A response which may lead to a <u>reduction</u> in uncertainty, namely the acquisition of information which allows the decision maker to determine the probabilities of possible outcomes, is discussed in Section 2.3.

be considered in the decision process. Scott (1967) proposes a second "coping response", stating that a decision maker lacking the ability to determine objective probabilities of possible outcomes' occurrence, may derive subjectively-based probabilities as a means of coping with uncertainty. Finally, Mack suggests that in extreme cases, decision makers may attempt to deny the existence of uncertainty in a decision situation by simply avoiding the act of decision.

In his model of administrative man, Simon (1957) outlines a decision maker's propensity to simplify the decision process by limiting the variables which are assessed before choosing a course of action. The decision maker attempts to define the decision situation in terms which are most understandable to him and thus, tends to concentrate on variables or factors with which he is most familiar. Similarly, Braybrooke and Lindblom (1963, p.90) suggest that decision makers explicitly simplify their assessments of incremental policy alternatives by limiting the number and type of possible consequences of these alternatives which will be considered. Accordingly, decision makers will "...often rule out of bounds the uninteresting (to them), the remote, the imponderable, the intangible, and the poorly understood, no matter how important". Thus, only consequences which can be quantified or which are understood <u>a priori</u> by the decision maker will tend to be considered during the decision process.

Mack (1971) proposes that a decision maker may likewise act to limit the alternatives he must consider when faced with uncertainty in a decision situation. In her view, the decision maker may be confused and perhaps distressed by his inability to predict the outcomes of alternative strategies, and consequently may attempt to reduce uncertainty by eliminating from consideration those strategies with the greatest attendant uncertainty. Mack's proposal is supported by Vannoy (1965) and Emery (1967), who found that individuals tended to redefine a complex decision task by emphasizing one or more situational variables to the exclusion of others. Not surprisingly, decision alternatives retained for consideration in the decision process tend to be those with which the decision maker is most familiar (Alexis and Wilson, 1969; Hage, 1980). Brown (1971), for example, suggests that decision makers may attempt to apply formalized organizational decision rules to an uncertain decision situation. Elements of the decision situation which are not covered by established procedures may be rejected or ignored in favor of those to which an organization's repertoire of decision rules can be applied. According to Brown (1971) the decision maker attempts to re-define the decision situation in order to use the organization's collective experience and administrative practices as the bases for assessing alternative courses of action.

A second possible response by decision makers to cope with uncertainty may be to use subjective estimates of possible outcomes as the bases for choosing a course of action. Since the decision maker cannot determine either the specific outcomes of a decision or the objective probabilities of their occurrence under conditions of uncertainty, he may use his general knowledge of the problem under consideration to subjectively determine the relative likelihood of a decision's outcomes (Richards and Greenlaw, 1972; Huber, 1983; Lathrop and Linnerooth,1983). These personal estimates or "subjective probabilities" of possible decision outcomes are then used to evaluate and rank alternative strategies in the same way that objective probabilities are used to compare expected outcomes of decision alternatives (Schlaifer, 1959).

In a similar vein, Ebert and Mitchell (1975) view the decision maker's judgement of alternative strategies' outcomes under conditions of uncertainty to be a cognitive act comprised of three components: 1) the decision maker's subjective evaluation of a decision's possible outcomes, 2) his subjective evaluation of the utility or desirability of the outcomes, and 3) his subjective estimates of the probability of these outcomes' occurrence. According to this view, the decision maker uses his personal knowledge and experience to derive what he believes is a comprehensive list of consequences arising from each alternative strategy. Having identified the range of possible consequences, the decision maker then uses some combination of personal and organizational values to evaluate the desirability of each outcome. Finally, the relative likelihood or probability of each outcome is subjectively determined, with the decision maker's knowledge or experience again serving as the basis of the assessment.

A somewhat extreme response to uncertainty in a decision situation might be the onset of passivity or an unwillingness to decide on the part of the decision maker (Mack, 1971). A decision maker may perceive that each alternative course of action could potentially result in a negative outcome, even though the specific magnitude or extent of the undesirable results may not be known. In these circumstances, there may be a tendency on the part of the decision maker to cognitively deny the fact of uncertainty in the decision situation by refusing to undertake the act of decision (Mack, 1971). The failure to decide may take the form of a temporary state of procrastination (Shull, 1970) or a more permanent "decision not to decide" (Mack, 1971). As a response to uncertainty, this state of passivity until either a superordinate demand for a decision is forced upon the decision maker or additional information concerning the outcomes is made available which reduces conditions of uncertainty to conditions of risk or certainty.

A decision maker's coping responses in the face of uncertainty may lead to the intrusion of selective biases in assessments of decision alternatives, thereby increasing the possibility of a decision resulting in unforseen or negative consequences. Scott (1967), for example, argues that subjective estimates of decision outcomes are based on the decision maker's experience and values, and thus reflect the personal biases of the decision maker. This biased view of possible decision outcomes may cause the decision maker to overlook or ignore consequences which he finds undesirable or of which he has little or no experience. This view is supported by Downs (1967) who found that decision makers will partially screen out data adverse to their interests and give undue preference to alternative courses of action most favorable to their interests. Similarly, Brown (1971) found government decision makers tended to reject aspects of vague decision situations which were not consistent with their personal beliefs, prejudices and values. Scott (1967) goes on to point out that a decision maker's biased view of the decision situation may lead to erroneous judgements of expected outcomes' probabilities. This is substantiated by Tverskey and Kahneman (1975) who reviewed aspects of judgements under conditions of uncertainty and found a number of systematic biases in decision maker's choices led to predictable distortions in decision markers' estimates of the probabilities of decision outcomes. Further support for this view can be found in Lathrop and Linnerooth's (1983) analysis of three assessments undertaken to evaluate the risks involved with a proposed liquid natural gas facility at Oxnard, California. Since few (if any) objective probabilities could be determined for possible risks or accidental events, Lathrop and Linnerooth found the assessors tended to use subjective judgements of probabilities derived from professional experience and values; as a result, the three assessments came to very divergent estimates of the overall risks attendant to the proposed LNG facility. Finally, Winkler (1967) and von Holstein (1971) have documented the tendency of decision makers in uncertain decision situations to express more confidence in their estimates of outcome probabilities than is empirically justified. In sum, the use of subjective estimates concerning the relative likelihood of outcomes in an uncertain decision situation may lead to biased assessments of alternative strategies and erroneous judgements of expected outcomes. A decision in these circumstances may result in unanticipated consequences or an outcome which may be considered undesirable by the decision maker.

A decision maker's efforts to cope with uncertainty by limiting the factors considered in a decision situation may also lead to an unanticipated or undesirable decision outcome. Mack (1971) suggests that by restricting the factors and processes which are considered during the decision process, a decision maker may in fact base his assessments of decision alternatives on an over-simplified view of the decision situation, thus enhancing the possibility of unanticipated or undesirable outcomes. In a similar vein, Shull _et al_ (1970) point out that the emphasis of decision makers on simplification of the decision situation may lead to distorted estimates of the outcomes associated with each strategy and therefore, the results of a decision may not be those expected by the decision makers. Support for this view is provided by Emery (1967) who, in his review of decision making in complex or ambiguous decision situations, identified a tendency for decision makers to focus selectively upon a problem situation, retaining aspects of the situation which were considered to be relevant while excluding other aspects. The set of factors considered relevant by the decision makers did not always reflect critical aspects of the original decision situation, and thus, the efficacy of selected courses of action in solving the problem at hand was reduced.

A decision maker's attempt to cope with uncertainty by selectively focussing on specific aspects of a decision situation appears to lead to distorted or extremely limited perceptions of outcomes which might be expected from a decision. In these circumstances, a selected course of action may not only result in outcomes which differ in magnitude from those expected by the decision maker, but as well may result in unanticipated or unwanted consequences.

Unlike decision makers' coping responses, which may detrimentally affect the assessment of decision alternatives or the possible outcomes of a decision, a decision maker's unwillingness to decide in the face of uncertainty may result in the suspension or termination of the entire decision process (Mack, 1971). The immediate effect of a decision maker's unwillingness to act might include the dissipation of research funding or other resources used for information-gathering (Shull _et al_, 1970). More importantly, however, the extended failure of a decision maker to decide may lead the decision maker to consider decision alternatives with no immediate intention of choosing one alternative, or to terminate the process and permanently avoid the selection of any course of action. It can thus be seen that an attempt by the decision maker to deny the fact of uncertainty in a decision situation not only fails to reduce uncertainty, but worse, allows the original problem to persist.

Attempts by decision makers to a) limit the scope of a decision situation, b) subjectively determine the relative likelihood of perceived outcomes, or c) deny the fact of uncertainty by refusing to decide, severely limit the effectiveness (or the extent to which desired outcomes are achieved) of a decision made under conditions of uncertainty (Ebert and Mitchell, 1975). If the decision process is assumed to be initiated in response to a specific problem, then the effectiveness of a decision can be seen as the degree to which the selected course of action resolves the original problem in a manner intended by the decision maker. According to this definition, a decision maker's unwillingness to make a decision is totally ineffective in resolving the original problem, since the refusal to decide allows the problem to remain intact. The effectiveness of decisions is only marginally increased in cases where the decision maker opts to limit the variables considered or form subjective estimates of possible decision outcomes rather than reduce uncertainty to a state of risk or certainty. In these situations, a course of action <u>may</u> be chosen which results in an outcome desired by the decision maker; however, it is also very likely that the decision will result in unanticipated or negative outcomes which exacerbate or otherwise fail to resolve the problem. Thus, the effectiveness of decisions under conditions of uncertainty may be severely constrained by responses invoked to cope with uncertainty.

2.3 Functional Information and Uncertainty Reduction.

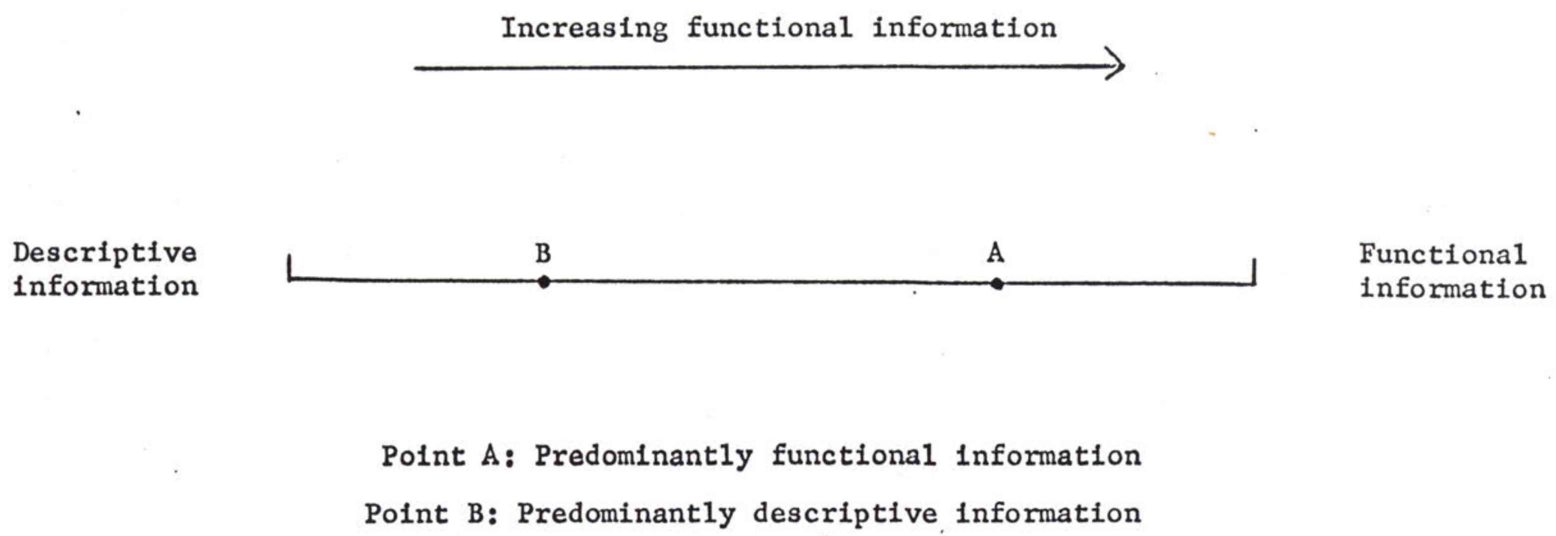
A state of uncertainty in a decision situation essentially reflects the inability of the decision maker to determine either a specific, determinate outcome or the probabilities of possible decision outcomes. Scott and Mitchell (1972, p.170) believe that "There is an inverse relationship between information and uncertainty", and suggest that the unpredictability of outcomes inherent in an uncertain decision situation may be reduced by the acquisition of information concerning the probabilities of possible outcomes. In their view, uncertainty in a decision situation arises when the interactions between the decision environment and actions associated with the implementation of a decision cannot be placed in a predictive framework; in other words, the decision maker cannot determine the explicit, causal relationships between systemic elements and processes which constitute the decision environment and actions carried out during the implementation of the decision. However, as Scott (1967, p.170) argues, "Information...structures an uncertain environment for the decision maker." In a similar vein, Scott and Mitchell (1972, p.175) propose that "The more uncertain a system the greater is its potential for varieties of behavior. Information introduces organization into the system---killing variety---thus making the system more predictable." According to these propositions, the acquisition of information allows a decision maker to develop a predictive framework or model of the decision situation incorporating the relationships between actions associated with the implementation of a decision and the elements and processes comprising the decision environment. If sufficient information can be gathered, these relationships can be specified within the model, thereby allowing a decision maker to determine the relative frequencies of occurrence of possible outcomes for each alternative course of action (Leblebici and Salancik, 1981). Thus, if sufficient information can be gathered and incorporated into a predictive framework, the model can be used to generate the possible consequences associated with each strategy-decision environment combination (Cleland and King, 1968). The acquisition of information during the decision process can therefore be such to increase the predictability of decision outcomes, or as Bridge and Dodds (1975, p.38) put it, "When information feeds back to the decision maker, uncertainty is transformed into risk...".

Clearly, information acquired during the decision process can reduce the uncertainty existing in a decision situation, thus increasing the effectiveness of the decision process. White (1969) and Dorcey and Hall (1981) suggest that the reduction of uncertainty in a decision situation is primarily dependent on the quality of information which is acquired. White (1969) proposes that two levels of information may be used in organizational decision making, which he terms "state" and "relational" information respectively. In his view, "state"-type information simply describes the state of affairs in some context: examples might include the state of the economy, the state of an organizational department, or the state of the environment. On the other hand, "relation"-type information specifies some connection or casual relation between states. To illustrate, the statement "An act X will result in the consequence Y", if indeed true, represents relational information specifying the causal link between X and Y. As White (1969, p.141) puts it, "'Relational' information allows us to deduce one set of propositions from another, whereas 'state' information contains no deductive element and is purely a means of identification."

In a similar vein, Dorcey and Hall (1981, p.8) propose that the information used in resource management decision making can be categorized as either "descriptive knowledge" or "functional knowledge". They state that a distinction between "...descriptive knowledge of [a system], which merely describes the elements of it, and functional knowledge, which goes beyond description of the elements to specify the cause-effect relationship between, i.e. involves processes". Like White's (1969) conceptualization of "state" information, descriptive knowledge in Dorcey and Hall's view refers to static descriptions of phenomena; examples in a natural resource context might include the size and type of wildfowl populations, the distribution of marsh plants, and the flow characteristics of riverine watersheds. Functional knowledge, on the other hand, is concerned with system relations or processes, examples might include the effects of riverine flow alterations on salmonid spawning or the effect of habitat reduction on wildfowl distribution.

Relation information or functional knowledge, rather than state information or descriptive knowledge, provides the key to reduction of uncertainty in a decision situation, or as Scott and Mitchell (1972) would have it, to an increased predictability of the systems under consideration in the decision situation. In an uncertain decision situation, a decision maker may acquire purely descriptive information and thereby increase his understanding of the actions associated with the implementation of a decision or elements of systems comprising the decision situation. However, since the relationships between activities arising from a decision and the systems comprising the decision environment cannot be determined from purely descriptive information, the inherent unpredictability of the decision sitution is not reduced and conditions of uncertainty continue to exist. On the other hand, functional information is directly concerned with causal relationships between actions and systemic elements or processes which may be involved in a decision situation. A decision maker who acquires functional information will enhance his understanding of the causal links between actions associated with a decision and the systems which may affect or be affected by a decision, and thus, will increase his ability to predict the possible consequences of a decision (Eckel, 1983). If sufficient functional information is acquired, the predictability of the decision situation may be increased to the point where probabilistic values can be determined for possible outcomes; in other words, a condition of uncertainty existing in a decision situation may be reduced to a condition of risk.

The quality of information available to a decision maker is seen by Dorcey and Hall (1981) as a spectrum ranging from purely descriptive to purely functional information (Figure 2-2). Between these extremes are points on the spectrum which indicate the availability of a combination of descriptive and functional information. For example, point "A" near the right end of the spectrum portrayed in Figure 2-2 indicates an amount of predominantly functional information which is sufficient for the decision maker to determine specific relationships between actions associated with a decision and the systems comprising the decision environment. Although the precise consequences of a decision cannot be specified, a probability value can be determined for each possible outcome of alternative courses of action. Conversely, point "B" near the left end of the spectrum indicates the availability of predominantly descriptive information which does not allow the decision maker to specify causal relationships between actions arising from the imple-



(Adapted from Dorcey and Hall, 1981)

FIGURE 2-2. QUALITY OF INFORMATION WHICH MAY BE AVAILABLE DURING THE DECISION PROCESS.

mentation of a decision and the decision environment. With only this information at hand, the decision maker cannot be sure of identifying all possible consequences of a decision, let alone determine the respective probabilities of possible outcomes.

The ability of decision makers to assign probabilities to possible effects of a decision and the attendant conditions of uncertainty, risk and certainty appear to be dependent on the amount of functional information available at the time of decision (Figure 2-3). A body of purely functional information allows the decision maker to specify the single determinate outcome for each alternative course of action, thereby allowing a decision to be made under conditions of certainty. Where the amount of functional information is sufficient for probabilities of possible decision outcomes to be determined, that decision can be made under conditions of risk. However, where the information available to the decision maker is purely descriptive, or where the body of functional information is not sufficient to determine causal relationships between actions associated with a decision and the systems in the decision environment, the decision will be made under conditions of uncertainty.

From the preceding discussion, it can be seen that limitations in the amount of functional data available at the time of decision curtail the decision maker's ability to predict the influence of the decision environment on

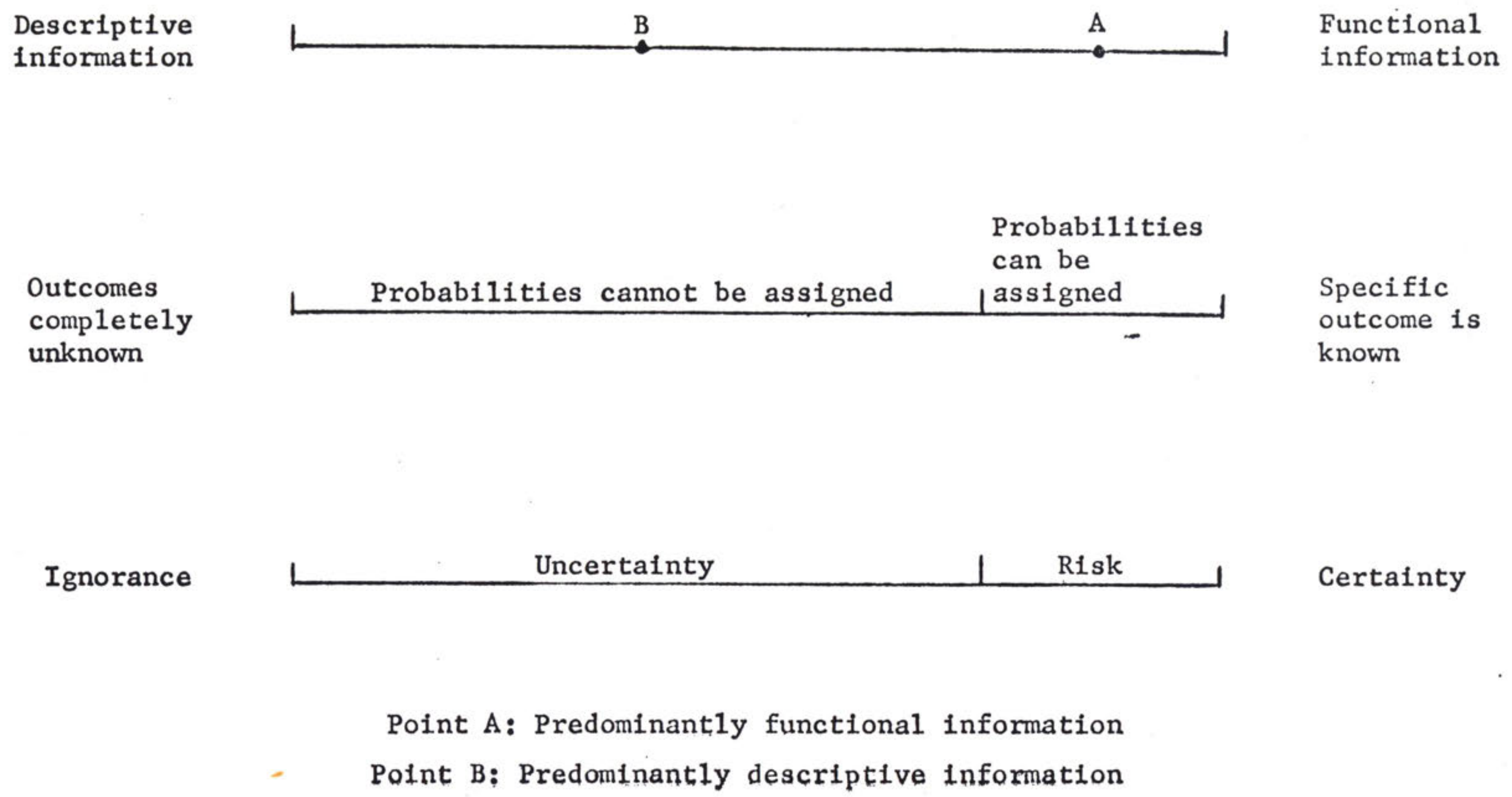


FIGURE 2-3. CONCEPTUAL RELATIONSHIP OF FUNCTIONAL AND DESCRIPTIVE INFORMATION TO CONDITIONS OF CERTAINTY, RISK AND UNCERTAINTY IN DECISION SITUATIONS.

the implementation of a decision and the concurrent effects of the decision on that environment. Where the available information is primarily descriptive in nature, the interrelationships between actions associated with a decision and the decision environment cannot be specified, and thus conditions of uncertainty may persist as a feature of the decision situation. In resource allocation decision making, the quality of available information and associated conditions of certainty, risk and uncertainty are critical factors determining the effectiveness of an allocation decision process. The effectiveness of a decision (the degree to which desired outcomes are achieved) is dependent on a) the decision maker's understanding of interrelationships between a proposed resource use and the social or ecological systems which may be affected, and b) his ability to predict the consequences of a particular allocation strategy. The quality of information (either descriptive or functional) which is available during the decision process determines whether these interrelationships and consequences can be specified, and thus, whether a selected allocative strategy will achieve desired results.

Unfortunately, the finite time and financial resources available to decision makers may act to limit the functional information which may be acquired. Once the decision process is underway, Bridge and Dodds (1975, p.52) believe insufficient time may be available to gather an optimum amount of functional information:

> "Even if "administrative man" did want to trace all the complex interrelationships...and gather all relevant information, he would not have unlimited time to do so. Many decisions have to be made very quickly relative to the time needed for adequate search."

In situations where a perceived conflict or crisis is imminent, or when superordinate public or political demands for a decision must be met, the time allotted for a decision is curtailed; consequently, the time available for information-gathering is reduced (Brown,1971).

Information-gathering might also be restrained by competing demands for the decision maker's time. A decision maker's responsibilities usually include a number of concurrent administrative tasks requiring some expenditure of the decision maker's time. If the decision maker perceives that time spent on a particular decision task detracts from his ability to carry out other administrative tasks, the amount of information deemed necessary for a decision may be reduced (Audley,1971). Thus, reductions in both the scope of search activities and the time allotted for information gathering can restrict the amount of functional information acquired by decision makers.

The financial costs of data gathering may also limit the decision maker's ability to acquire functional information. Dorcey and Hall (1981) argue that functional information can only be generated through hypothesis-testing and experimentation. Experimental research can be very expensive, and as Audley (1971) points out, other administrative tasks must also be funded within the constraints of the decision maker's budget. The decision maker must therefore weigh the utility of a complete body of functional information against the financial costs of acquiring that data (Scott and Mitchell,1972). Bridge and Dodds (1975,p.52) further observe that :

> "Search [for information] may be subject to diminishing marginal returns in which case there would come a point when additional expenditure on it would not be economic. It is perhaps therefore simply not cost-effective to make decisions which are...based on complete information."

Thus, in addition to time constraints, the financial costs of obtaining functional information and the limited finances available for such an undertaking may limit the functional data which can be acquired by the decision maker.

2.4 Summary

Decision making can be viewed as a purely rational exercise involving the choice of an appropriate course of action based on perfect knowledge of the outcome of a decision, or as a subjective exercise involving a choice based on limited or imperfect knowledge of the decision's consequences. A purely rational decision is rarely possible in actual decision situations and decisions will most likely be made on the basis of a partial understanding of the type or magnitude of consequences which might occur.

The concepts of "certainty", "risk", and "uncertainty" are related to a decision maker's ability to determine the relative likelihood or probabilities of possible outcomes of a decision. A condition of certainty in a decision situation reflects the ability of the decision maker to predict a specific outcome for a selected course of action, while conditions of risk and uncertainty are portrayed as the respective ability or inability of the decision maker to determine the probabilities of possible outcomes.

The possible responses by decision makers to cope with or deny uncertainty lead to ineffective decision making. Therefore, the reduction of conditions of uncertainty to those of risk appears preferable to a decision maker's coping or denial strategies. Uncertainty reduction is linked to the quality of information available to the decision maker during the decision situation. The availability of primarily descriptive information will prolong conditions of uncertainty in a decision situation, while the acquisition of functional information will reduce uncertainty to the point where a decision can be made under conditions of risk or certainty. Unfortunately, time and financial constraints

CHAPTER 3

VANCOUVER ISLAND SMALL SCALE HYDROELECTRIC DEVELOPMENT AND SALMONID SPAWNING HABITAT REQUIREMENTS

3.1 Introduction

Numerous streams on Vancouver Island provide freshwater habitats essential to the reproductive success of spawning adults and the subsequent viability of juveniles. The importance of these habitats to salmon production is widely recognized, and substantial support has been given by public groups, the commercial and sports fishing industries, and government agencies to the preservation and enhancement of freshwater salmonid habitats (Wood,1976; Fisheries and Marine Service,1978; Pearse, 1982; Department of Fisheries and Oceans, 1984). However, a decline in absolute numbers of fish in some areas, attributable in part to degradation or destruction of salmonid habitat (Pearse,1982), has re-emphasized the need for protection of existing instream habitats (Department of Fisheries and Oceans,1983).

This chapter examines the operations of small-scale hydroelectric (SSH) facilities which may result in alterations of downstream flow regimes and outlines hydraulic parameters which comprise the spawning habitat of Pacific salmon species. The analysis establishes the necessary background to address the research argument outlined in Chapter 1. The chapter is divided into two parts. Section 3.2 presents an overview of the study area and potential SSH sites, and describes the nature of Vancouver Island's electrical demand and possible role of SSH facilities in meeting peak load requirements. The section concludes with an outline of possible streamflow alterations caused by peaking power generation at SSH facilities. Section 3.3 reviews stream depth and velocity characteristics which constitute spawning habitats utilized by Vancouver Island salmon.

3.2 Potential Small Scale Hydro Development on Vancouver Island.

3.2.1 Physical Setting and Distribution of Potential SSH Peaking Facilities.

The general relief of Vancouver Island is governed by two major physiographic features: 1) the Insular Mountains extending from the Queen Charlotte Islands south through Vancouver Island, and 2) the Coastal Trough stretching from southeastern Alaska along the east coast of Vancouver Island to the Puget Sound area. The topography is dominated by the Vancouver Island Mountain Range which, as part of the Insular Mountain chain, extends through the western and interior regions of the Island (Figure 3-1).

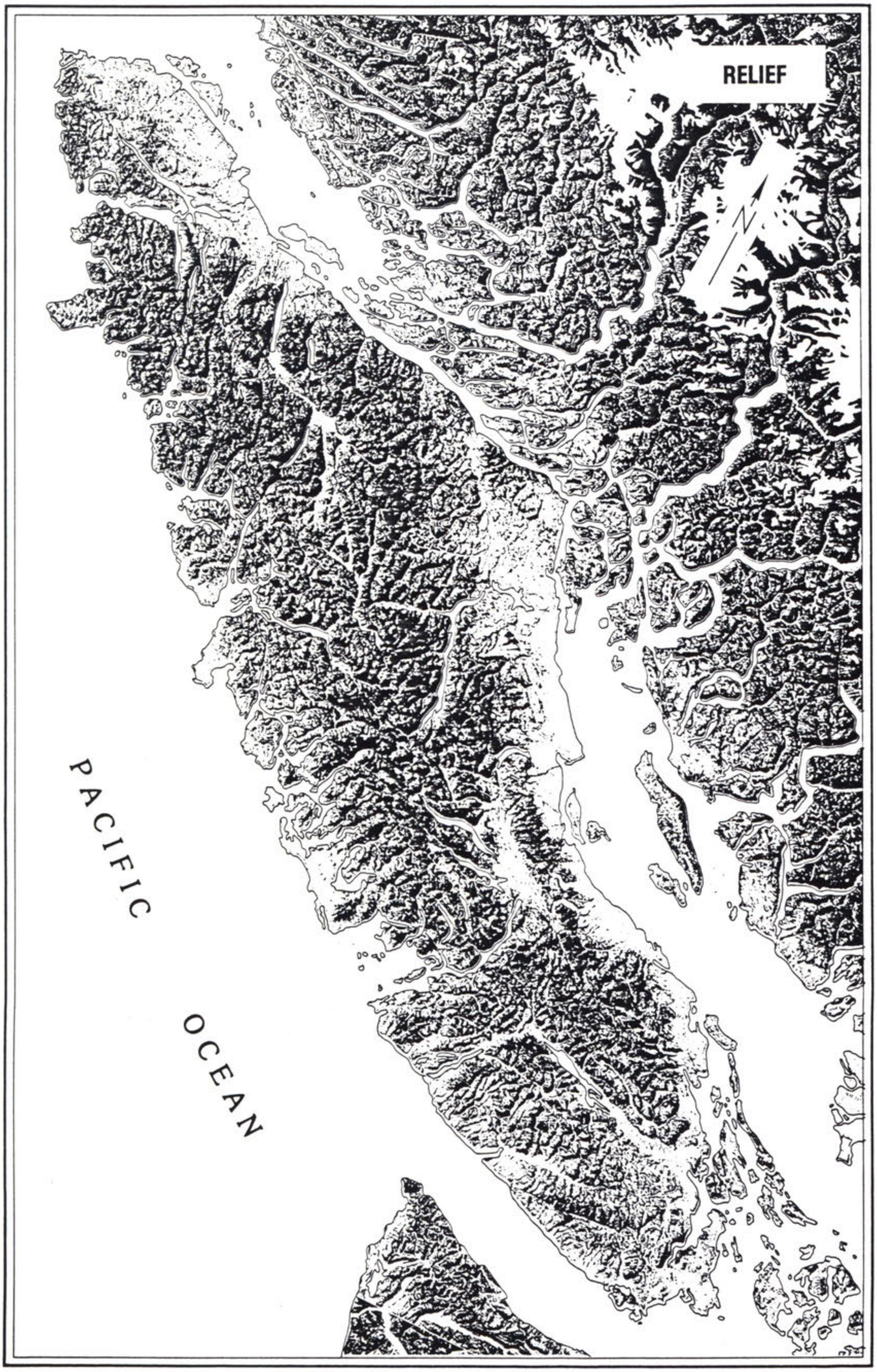


FIGURE 3-1. VANCOUVER ISLAND PHYSICAL RELIEF. (Source: Foster, 1979)

The Vancouver Island Mountains are comprised of a rugged chain of highlands reaching elevations of 2000 m or more at several locations in the central interior. In contrast to the mountainous interior, a series of coastal lowlands nearly encircle the Island (Foster,1979).

Because of the generally high relief and westerly pattern of atmospheric circulation, Vancouver Island receives heavy (if seasonal) precipitation. Most of the Island's precipitation falls between October and March (Figure 3-2), usually in the form of rain along the coast and lower elevations and as snow during the winter at higher elevations. Conversely, a number of climatic factors combine to produce a marked summer minimum in precipitation, particularly between May and August (Tuller,1979). Mean annual precipitation is greatest on the west coast and in the interior regions where the orographic uplift of moist air induces precipitation at higher elevations. Significantly less precipitation is recorded on the east and south regions of the Island which lie in the rainshadow of the Vancouver Island Mountains and the Olympic Mountains in northwest Washington.

Much of Vancouver Island's precipitation is returned to the ocean by swift, relatively short rivers whose drainage networks originate in the mountainous interior of the Island. Discharge in Vancouver Island streams and rivers fluctuates over the course of a year in response to seasonal changes in precipitation. However, unlike rivers

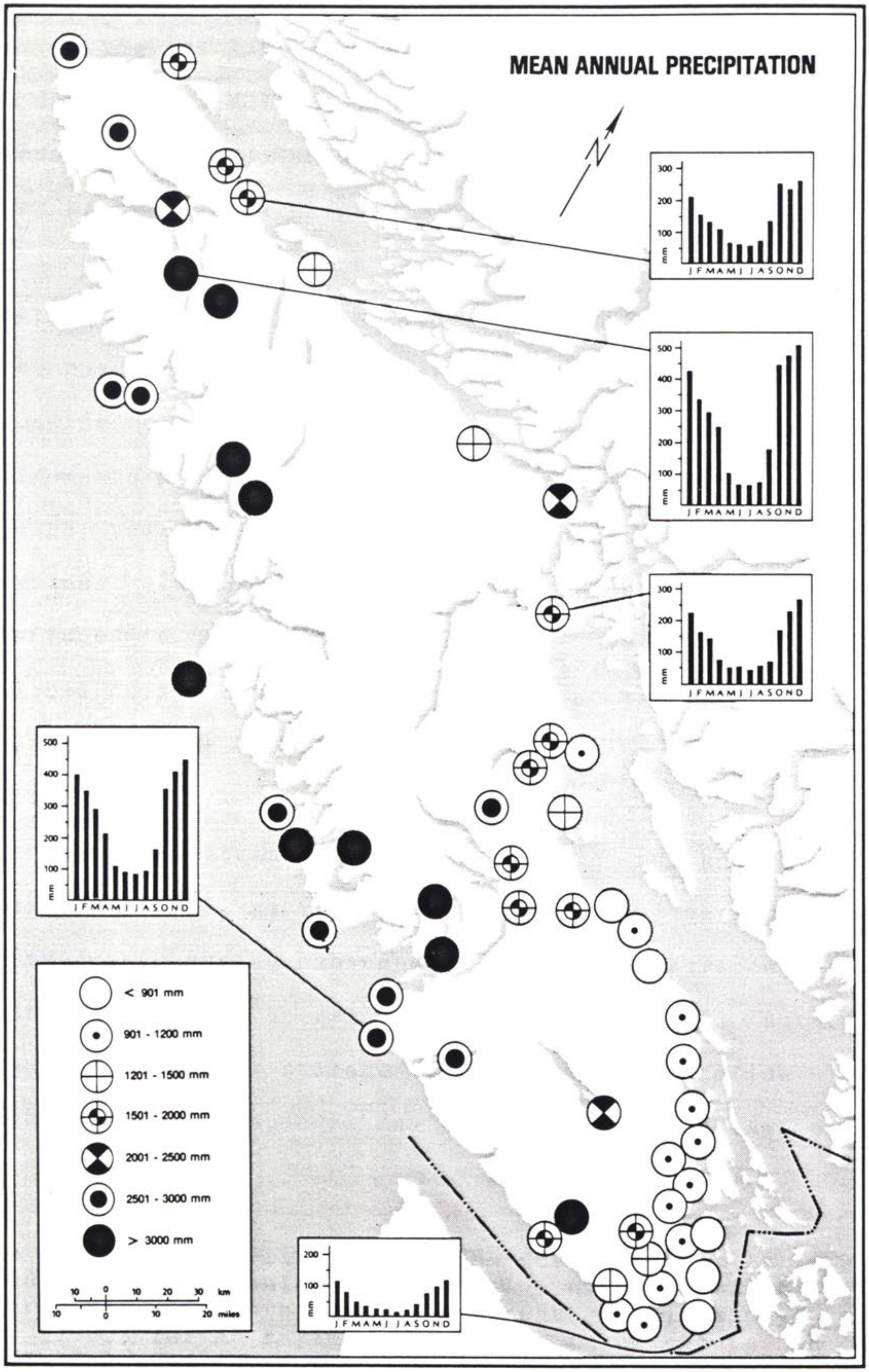
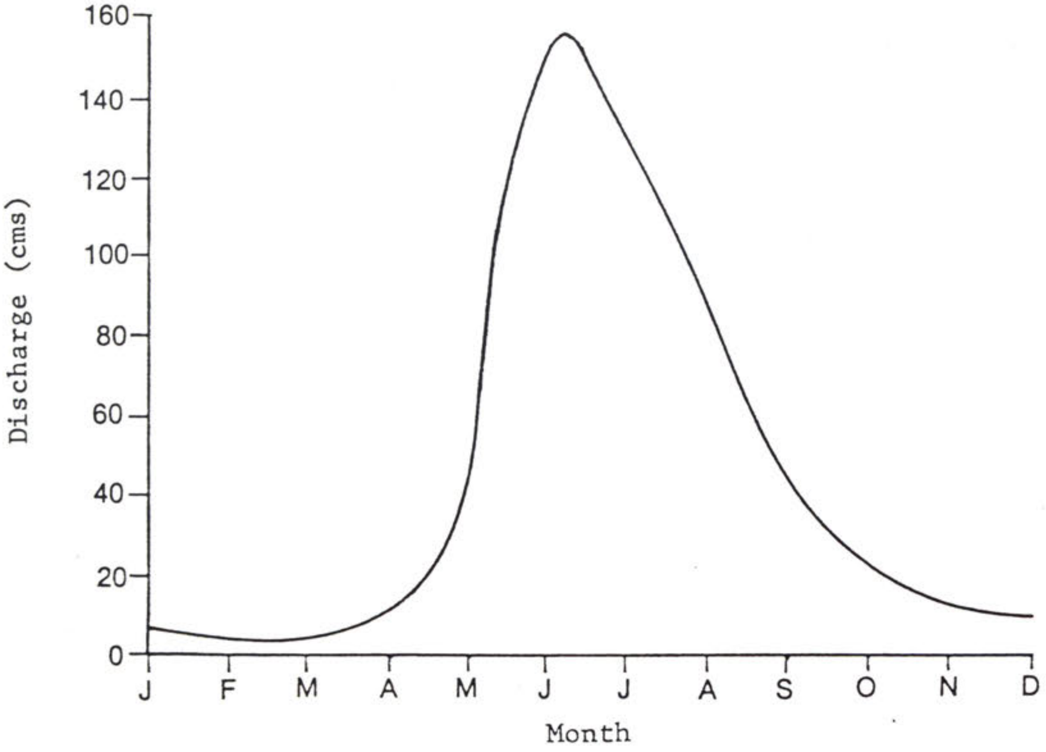


FIGURE 3-2. SPATIAL AND TEMPORAL DISTRIBUTION OF PRECIPITATION, VANCOUVER ISLAND. (Source: Tuller, 1979)

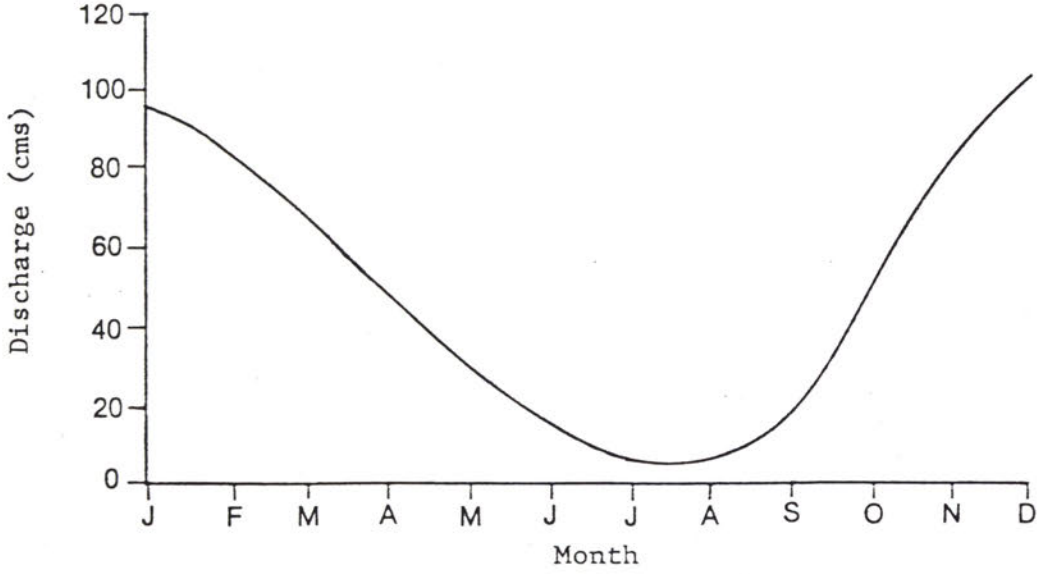
in the interior of the province whose peak discharges occur during the late spring and middle summer months, peak discharges of Vancouver Island rivers tend to occur between October and March, reflecting the heavy fall and winter precipitation (Figure 3-3).

A cursory examination of the general topography and climate of Vancouver Island suggests that SSH developments may be possible in certain areas. For SSH developments to be considered feasible, however, two specific physical requirements must be satisfied[4]. First, there must be adequate, year-round streamflow to support proposed SSH operations. In unregulated streams subject to seasonal variations in discharge, sufficient water must be available during low-flow periods to sustain hydroelectric generating operations. In some cases, water can be stored in upstream lakes or reservoirs to moderate seasonal fluctuations in stream discharge levels. During periods of high discharge, part of the streamflow may be stored or impounded and, during subsequent low-flow periods, the impounded water can be released to augment the natural streamflow. Where storage of excess streamflow is possible, SSH developments may be feasible on streams or

[4] The overall viability of SSH developments is also dependent on economic, technical and institutional requirements which are beyond the scope of this study; see James (1982) for a review of these requirements in a British Columbia context.



a) Fraser River at Red Pass



b) San Juan River Near Point Renfrew

(Source: Environment Canada, 1983)

FIGURE 3-3. MEAN MONTHLY DISCHARGE, FRASER RIVER (EASTERN BRITISH COLUMBIA) AND SAN JUAN RIVER (VANCOUVER ISLAND).

rivers whose natural flows would otherwise be insufficient for year-round hydro operations (Warnick, 1984).

The second physical requirement which must be satisfied is that the gradient or slope of the stream under consideration provides a sufficient "head" for a proposed SSH facility. The available head at a potential SSH site can be simply defined as the difference in elevation between the penstock intake level and turbine (Figure 3-4). In conjunction with the available discharge, this difference in elevation determines the amount of energy a flow of water can produce[5]. The power equation indicates that a very high head can compensate for a low level of discharge to produce an acceptable amount of power; conversely, a high level of discharge

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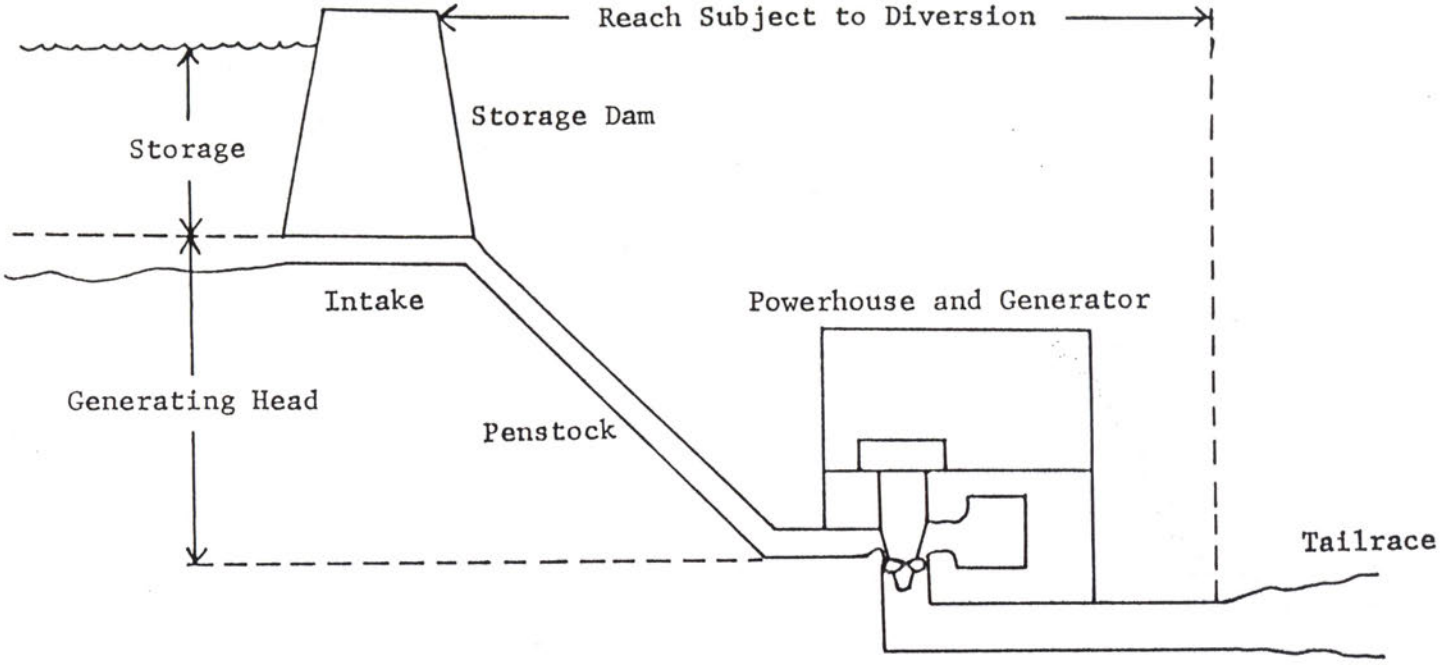
[5] The maximum potential water power available at a site is proportional to both the size of the stream discharge and the available head height. The relationship is indicated in the following equation:

$$P_{MW} = pqQHn$$

where P_{MW} = power output in megawatts
p = density of water, kg/m^3
q = acceleration of gravity, $9.8\ m/s^2$
Q = stream discharge, m^3/s
H = available head, m
n = plant efficiency, decimal percentage

Since the values p,q, and n are normally constant values, it can be seen that any increase in either the stream discharge (Q) or available head (H) will increase the potential power output of the site.



(Source: Loar and Sale, 1981)

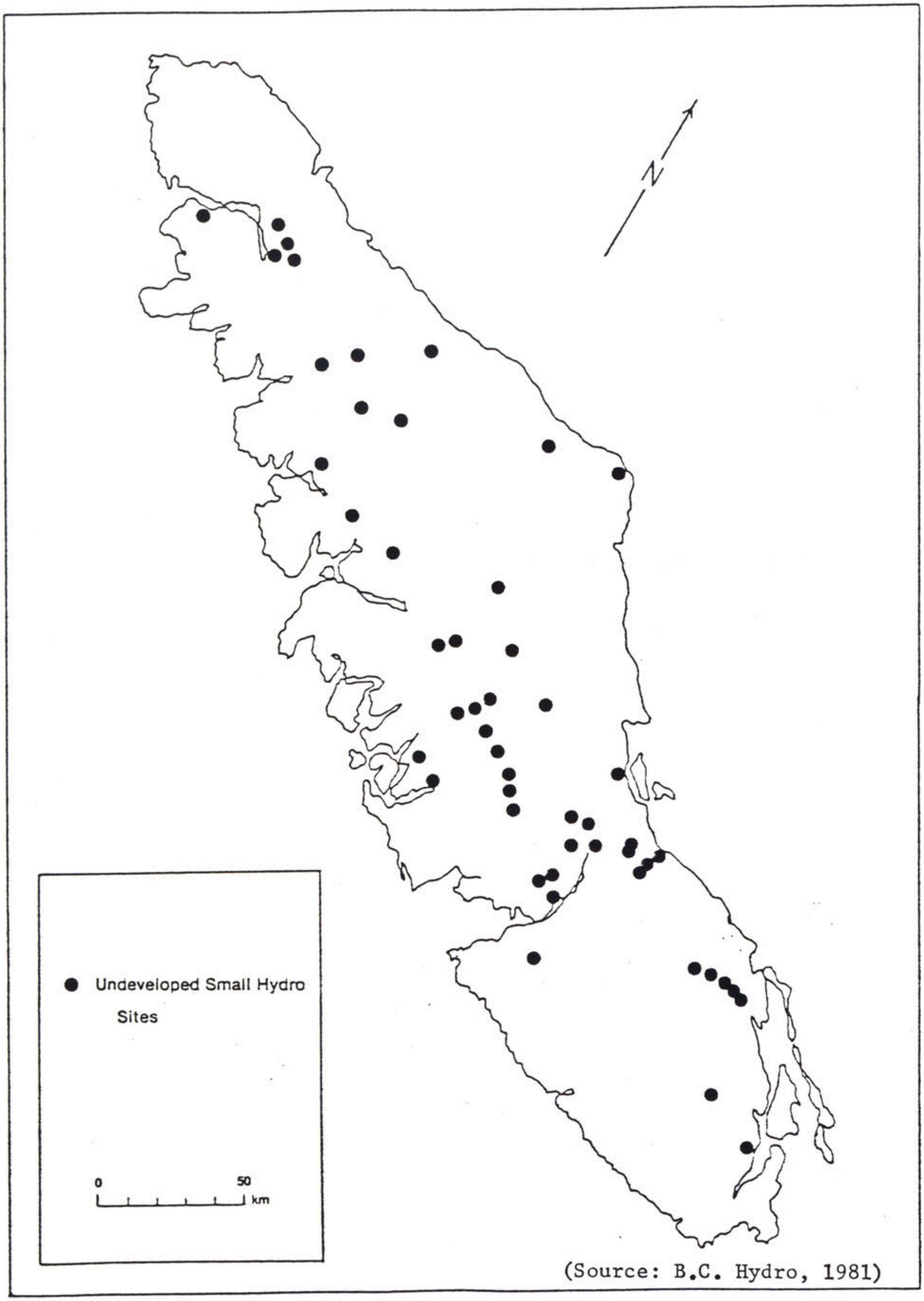
FIGURE 3-4. GENERAL CHARACTERISTICS OF SMALL SCALE HYDROELECTRIC FACILITIES.

must be available to compensate for a low head elevation in order for an SSH facility to be considered at that particular site.

In addition to the basic requirements of head and streamflow, efficient production of peaking power at SSH facilities depends on two conditions: 1) during the generation phase of SSH operations, the full generating capacity of the plant must be utilized to the greatest possible extent, and 2) it must be possible to adjust the volume of water discharge through the plant in order to generate the electricity required during periods of peak demand (Noyes,1980; Warnick,1984). If left unregulated, natural streamflow may not always provide sufficient water to enable the full generating capacity of the SSH plant to be utilized; as well, unregulated flow through an SSH generating plant will not allow power production to vary in response to changes in peak load. For these reasons, some form of water storage is required to facilitate efficient peaking power generation (Noyes,1980; Warnick,1984). Accordingly, reservoirs must be created in the vicinity of the SSH plant, either by closing the downstream end of a natural riverine basin or by damming the outlet of an upstream lake. The capacity of these reservoirs determines whether "storage" or "pondage" capabilities are available. "Storage" refers to the long-term impoundment of water in large-volume reservoirs to moderate seasonal fluctuations in water availability and meet seasonal variations in energy demand, while "pondage" refers to short-term impoundments in low-capacity reservoirs to meet daily fluctuations in energy demand.

Inventories of British Columbia's undeveloped hydropower resources have identified 67 sites on Vancouver Island with suitable combinations of head and streamflow for SSH developments (White,1919; British Columbia Water Resources Branch,1954; British Columbia Hydro and Power Authority,1981). Of these potential developments, 52 sites were found to have storage or pondage capabilities (B.C. Hydro,1981) and thus can be considered as suitable sites for SSH peaking power facilities. The majority of these potential SSH sites are located in the western and interior regions of the Island where the mountainous terrain, high precipitation, and numerous inland lakes provide high head elevations, substantial stream discharge and storage capabilities at several locations (Figure 3-5). Several potential sites in these regions are located on low-discharge streams where very high heads (150m or greater) are available to compensate for the lack of streamflow; as well, a number of small lakes or natural river basins provide pondage capabilities for eight SSH facilities in the interior and western regions.

Low precipitation in the rainshadow areas of southern and eastern Vancouver Island restricts the number of streams with sufficient year-round flow for small hydro



(Source: B.C. Hydro, 1981)

FIGURE 3-5. POTENTIAL SMALL SCALE HYDROELECTRIC SITES SUITABLE FOR PEAKING POWER DEVELOPMENTS ON VANCOUVER ISLAND.

developments. In the highlands to the west of the eastern coastal margin, several potential SSH developments are situated on low-discharge streams where (as was the case with similar sites in the western and interior regions) very high heads are available to compensate for the low streamflow. Conversely, potential SSH sites in the eastern coast lowlands tend to be located on larger rivers whose substantial discharges compensate for relatively low head elevations. Storage capabilities necessary for peaking power generation at eastern SSH sites are provided by several lakes in the eastern interior.

In the northern region of Vancouver Island, the heavy precipitation and runoff cannot compensate for the very low head elevations found in the flattened relief of the Nahwitti Lowlands. Thus, no feasible SSH sites were identified north of the Quatsino Sound area.

3.2.2 Vancouver Island Electrical Demand and the Suitability of SSH for Peaking Power Generation.

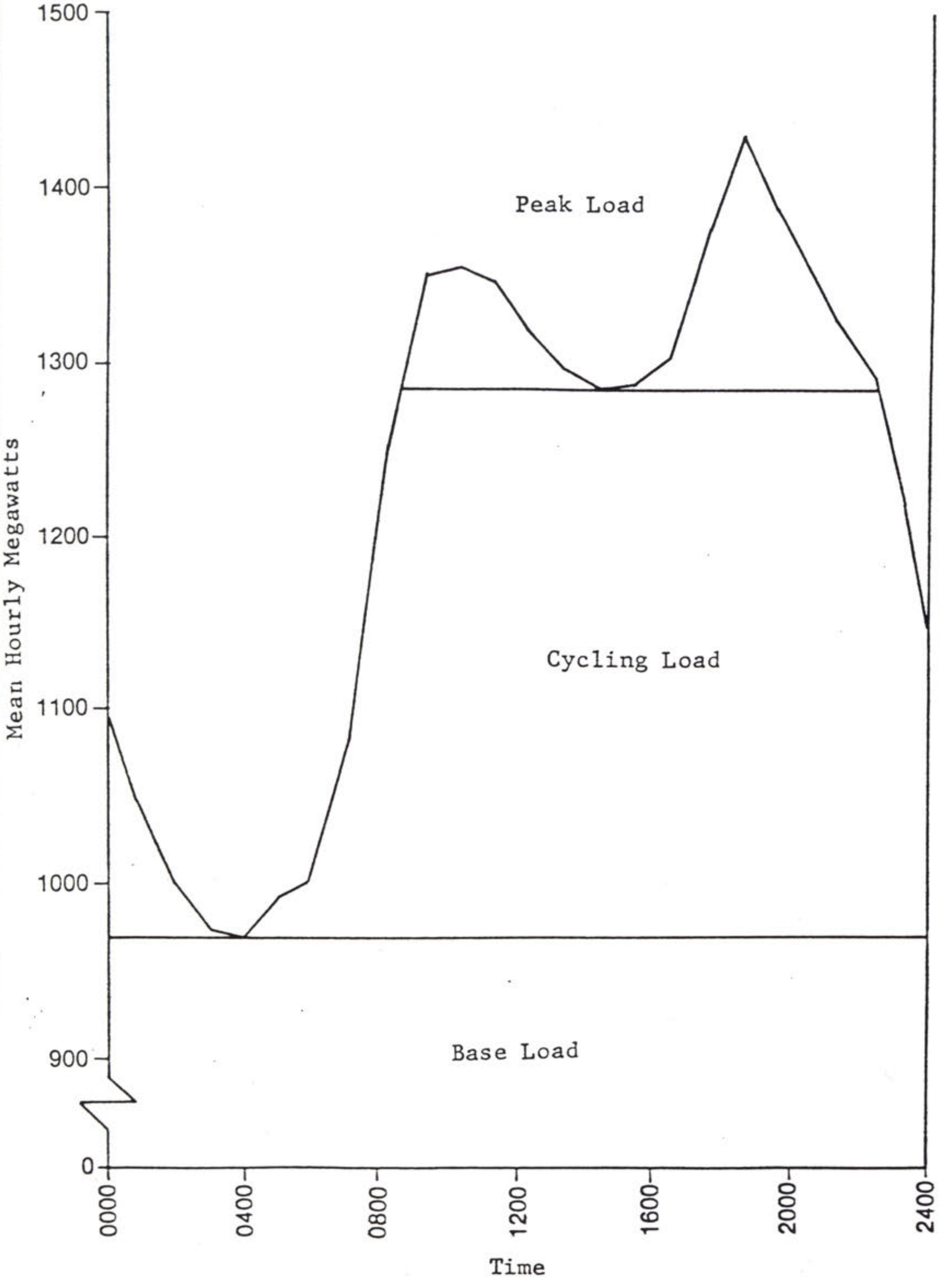
Before discussing the possible contribution of SSH facilities to Vancouver Island's future peaking power requirements, it is first necessary to outline the nature of electrical demand on the island. A primary concern of electrical energy producers is that the supply of power at any given time be sufficient to meet quantitative and temporal variations in electrical demand. The demand for electricity (or "system load") is rarely constant throughout the day or year. Manners (1964, p.126) points out that "Patterns of living, variations in the weather, and the nature of industrial processes all make for continuing changes in energy needs, which in aggregate create variable markets [for electricity] through time ...". On Vancouver Island, these factors cause the British Columbia Hydro and Power Authority (B.C. Hydro) to substantially modify the amount of power available during the course of a day or throughout the year in order to meet the requirements of industrial, commercial and residential customers.

B.C. Hydro's Vancouver Island supply system provides power to essentially three groups of customers, each with distinct differences in the amount and timing of electricity they require. Heavy industrial customers (such as sawmills or pulp and paper mills) tend to operate continuously and thus require a relatively constant amount of electricity throughout a 24-hour period. Light industries and commercial establishments normally operate for just eight hours each weekday and suspend operations on weekends; thus the electrical demand for these users is greatest between the hours of 0800 and 1700 each weekday. Residential customers use electricity primarily for cooking, heating and lighting; electrical demand is thus greatest between the hours of 0700 and 0900, 1100 and

1300, and 1700 and 2000 (E. Benedictson, pers.comm.,1985).

The combined electrical requirements of Vancouver Island customers produce a highly consistent daily pattern of demand (Figure 3-6). The minimum daily system load usually occurs between the hours of 0300 and 0500, a level of demand corresponding to the requirements of industrial customers operating around the clock. Between 0600 and 1000, the system load increases sharply as light industrial, commercial and residential customers begin to use electricity. This initial demand peak decreases between 1300 and 1400, indicating a reduction in residential usage; however, increased residential use of power for cooking, lighting and heating leads to a second peak between 1700 and 2000 (this load peak is moderated by a concurrent reduction in demand due to the termination of commercial and light industrial operations at the end of a working day). After 2000 the residential demand for electricity steadily decreases until the average demand reaches its minimum level.

In addition to daily fluctuations in demand, B.C. Hydro's Vancouver Island supply system must also provide for seasonal variations in overall power usage. The total level of demand increases steadily from early October to a maximum in January as reduced daylight and colder ambient temperatures promote greater usage of electricity for lighting and heating by commercial and residential customers (Figure 3-7). Conversely, demand generally

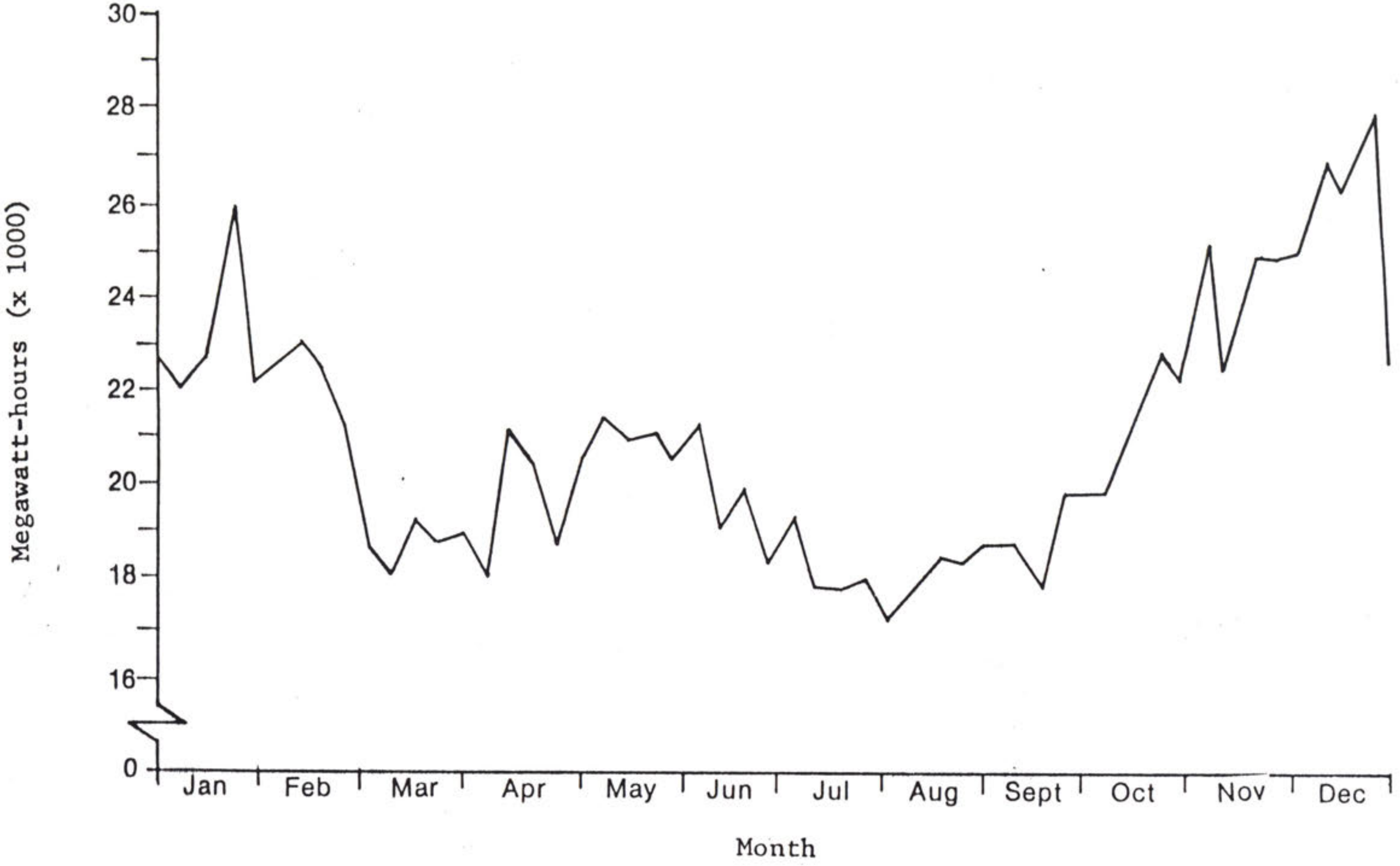


(Source: Erik Benedictson, B.C. Hydro, pers. comm., 1985)

FIGURE 3-6. VANCOUVER ISLAND PEAK LOAD DAY (DECEMBER 19, 1984).

decreases between early February and early May as available daylight and ambient temperatures increase. Since Vancouver Island's summer temperatures are seldom high enough to promote widespread use of commercial and residential air conditioning, there is normally little or no increase in demand between July and late August as might be the case in the southern interior of the province (E. Benedictson, pers.comm.,1985). Thus, the peak seasonal load essentially occurs between October and April, while a relatively consistent minimum load is evident between May and September.

The pattern of electrical use over a 24-hour period has prompted utilities to recognize three distinct categories of electric demand: base load, cycling load and peak load. The base load is defined as the sustained and essentially constant demand for electricity, the level of which is equivalent to the amount of power required for continuous industrial operations plus the minimum requirements of residential and commercial customers (Wilson and Jones,1974). On Vancouver Island, the base load is equivalent to the supply system's minimum demand evident between the hours of 0300 and 0500 (Figure 3-6). Cycling load is defined as the minimum amount of electricity in excess of the base load (up to but not including peak loads) required by residential, light industrial and commercial customers roughly between the hours of 0700 and 2400. As indicated in Figure 3-6, the



(Source: B.C. Hydro Logs--Hourly Readings and System Status, 1984)

FIGURE 3-7. VANCOUVER ISLAND MIDWEEK 24-HOUR TOTAL SYSTEM LOADS, JANUARY TO DECEMBER, 1984.

level of demand evident between 1500 and 1600 hours represents the approximate upper limit of the cycling load on Vancouver Island. Finally, a peak load can be defined as the level of electrical demand in excess of the cycling load. The Vancouver Island power supply system normally experiences two peak load periods, the first occurring between the hours of 0800 and 1300 and the second occurring between 1600 and 2100.

At present, Vancouver Island's overall base, cycling and peak load requirements are met by B.C. Hydro's supply system, which combines power transmitted from the mainland with electricity generated by hydro facilities located on the Island. Base load requirements are met with power transmitted via the high-voltage Cheekye-Dunsmuir and Arnott-Duncan transmission lines to Vancouver Island from the mainland grid. Cycling and peak load requirements are met with power generated at the Strathcona, Ladore Falls, Ash River, Puntledge, John Hart and Jordan River hydro facilities on the Island. Although the current reserve capacity of Vancouver Island's electrical supply system can accommodate some increase in peak load, more peaking power may be required at some point in the future, depending primarily on the magnitude of population and/or industrial growth on the island (E. Benedictson, pers.comm.,1985).

For a number of reasons, extensive SSH development could be a most efficient means of meeting Vancouver

Island's future peaking power requirements. First, a significant amount of peaking power could potentially be produced at SSH sites where natural streamflow can be impounded. If all 52 sites with storage or pondage capabilities were developed, approximately 440 MW of generating capacity would be available to meet peaking power requirements (B.C. Hydro,1981). Since the present maximum peak load on Vancouver Island is about 200 MW, the potential generating capacity of SSH peaking plants could meet considerable increases in Vancouver Island's future peak load.

Second, the sheer number of potential SSH peaking power developments and the inherent variety of possible generating capacities at or between these sites facilitates the development of small blocks of generating capacity in response to gradual increases in the peak load (Rockingham,1979). This ability to develop the Island's SSH generating potential in phases or increments enables B.C. Hydro to avoid the problem of an over-supply of power while ensuring that the development of peaking power supply keeps pace with the rate of increasing demand.

Third, power production at hydro facilities generally is very well suited to meeting rapid changes in energy demand. Generating operations at hydro plants can be increased or decreased almost instantly, unlike thermal or nuclear power plants which require several hours of "start-up" time before generation operations can begin.

As well, the operations of several hydro generating facilities can be simultaneously governed by way of a centralized control centre; thus, a series of SSH plants linked to some form of centralized control (which presently exists at the B.C. Hydro Duncan substation) could very easily have their generating operations adjusted to meet rapid charges in peak demand (Kahn,1978).

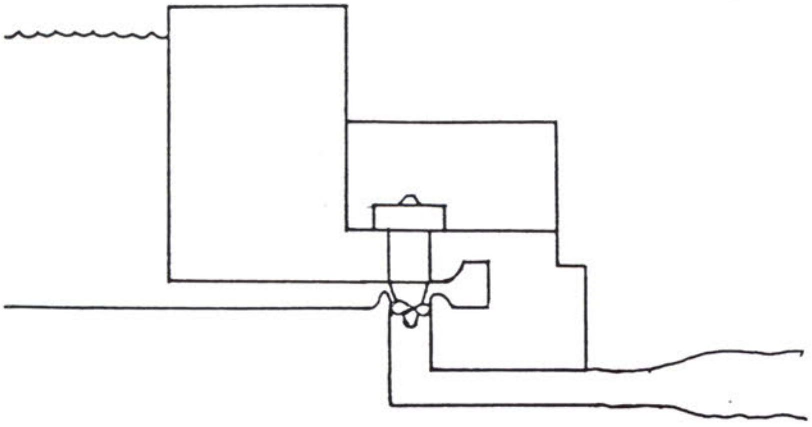
Finally, SSH facilities' seasonal ability to produce peaking power on Vancouver Island corresponds with the seasonal pattern of electrical demand. The period of peak stream or river discharge is generally congruent with the months of greatest electrical demand (see Figures 3-3 and 3-7). Since the amount of power which can be produced at a hydro facility increases with additional stream discharge, maximum peaking power can be generated at SSH facilities during the period of greatest peaking power demand.

The eventual role of SSH can thus be defined in terms of its ability to meet a specific segment of Vancouver Island's future electrical requirements. Because of the present surplus in electrical power on Vancouver Island, the potential generating capacity of SSH developments will likely remain superfluous to B.C. Hydro's base and cycling power requirements. However, as a source of peaking power, SSH could become an important addition to the Island's future electric supply system.

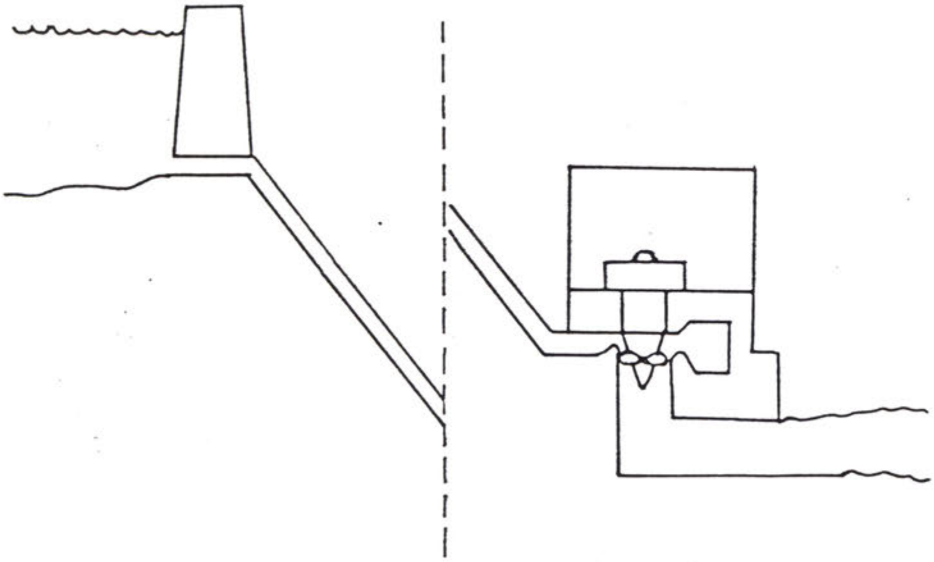
3.2.3 Alterations in Flow Regimes Below SSH Peaking Power Developments.

The effects of SSH peaking power developments on downstream flow regimes may be temporal or spatial in nature and depend on several factors including natural river flows, physical configuration of the reservoir-generating plant complex, the amount and timing of water impoundment, and the daily pattern of peaking power generation. Localized changes in streamflow may occur as a consequence of the spatial separation of reservoirs and associated generating facilities. The location of generating plants relative to upstream reservoirs varies according to site-specific streamflow and terrain conditions. In the simplest case, the amount of water available for generation purposes may be sufficiently great that the head elevation between the intake and turbine can be used to produce a desired amount of power (Figure 3-8a). At these sites, the generating plant (or "powerhouse") is situated at the base of the reservoir dam and thus, the spatial alteration of streamflow between the reservoir and powerplant is minimal. However, if more head is required to compensate for reduced water supplies, the powerhouse may be situated at a lower elevation some distance downstream from the reservoir, thereby necessitating diversion of water from the reservoir to the

a) Powerhouse incorporated into reservoir dam structure



b) Powerhouse located downstream from reservoir



(Source: Warnick, 1984)

FIGURE 3-8. SMALL SCALE HYDRO FACILITY WITH a) POWERHOUSE INCORPORATED INTO THE RESERVOIR DAM STRUCTURE AND b) POWERHOUSE LOCATED DOWNSTREAM OF THE RESERVOIR.

generating plant by means of a conduit or penstock (Figure 3-8b). Depending on the slope of the river valley and the head elevation required, a powerhouse may be located up to 5 km downstream from the associated reservoir (B.C. Hydro,1981). Although some water is usually allowed to spill from the reservoir into the natural stream channel, the reach of river between the dam and powerhouse may be subject to very low flows if the majority of available water is diverted through penstocks from reservoirs to associated generating plants.

While a portion of a stream may be affected by localized spatial alterations in streamflow, the entire reach of a river downstream of an SSH development can be affected by temporal changes in flow patterns. The impoundment and release of water for storage and power generation purposes may result in long and short-term changes in flow regimes below SSH reservoirs and generating plants. Long-term modifications of streamflow are characteristic of SSH developments utilizing reservoirs with large storage capacities (Loar and Sale,1981; Langford,1983). At these facilities, water can be impounded during high-flow periods to augment low flows during the summer months. The cycle of water storage and release reduces the amplitude of seasonal discharge, thereby creating a more uniform annual discharge pattern below the hydro site. On Vancouver Island, 44 of 52 potential sites for SSH peaking power developments were found to have storage capabilities, usually in the form of upstream lakes whose outlets could be dammed to impound water during the peak discharge period between October and early April. Below the reservoir dams at these sites, stream depth and velocity would probably be substantially reduced from natural levels during the period when streamflow is impounded. However, during the summer months when natural flows are augmented with water released from these reservoirs, stream velocity and depth below the generating facility would likely be greater than what might be observed under natural conditions.

At the eight remaining potential sites for SSH peaking facilities, impoundment capabilities are limited to small-capacity pondage reservoirs. Long-term alterations of streamflow would not be expected below these facilities simply because the limited capacities of these reservoirs would not be sufficient to store large volumes of water during the annual high-flow period. Thus, seasonal variations in stream discharge below these facilities would not be modified to any appreciable degree by impoundment of streamflow in pondage reservoirs.

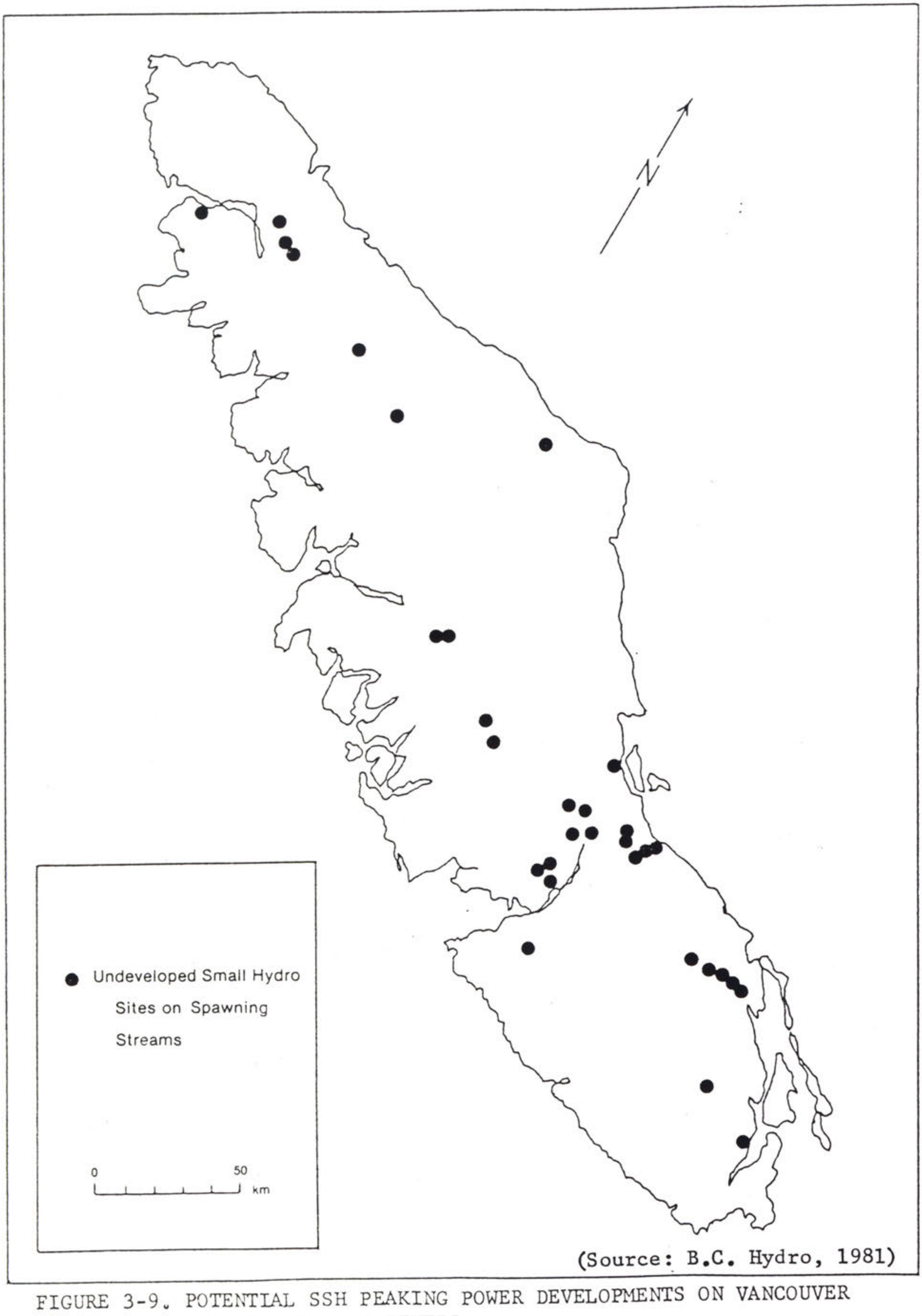
Short-term alterations of streamflow can be expected at all SSH facilities engaged in peaking power generation, regardless of the storage or pondage capabilities of associated reservoirs. Since the demand for peaking power arises only during specific times in a 24-hour period, water is impounded during off-peak hours and released during periods of peak demand. Stream depths and velocities below SSH generating plants could therefore be greatly altered over a span of several minutes or hours depending on the magnitude and duration of generating operations at individual facilities. While the discharge levels observed below generating plants over a 24-hour period may be equivalent to those recorded in unregulated streams, (which may be subject to large variations in discharge due to storm precipitation and subsequent runoff), peaking operations dramatically increase the frequency and rate of change in discharge levels relative to natural discharge patterns (Loar and Sale,1981). Thus, unnaturally rapid and numerous short-term changes in stream depths and velocities would likely occur during periods when peaking power is generated, while a more consistent level of stream discharge would be observed during off-peak hours when water is being impounded.

3.3 Pacific Salmon Spawning Habitat Requirements

Unregulated streams or rivers are characterized by streamflow conditions which, while highly variable, provide very specialized environments for instream organisms. Through millennia of evolutionary adjustments, organisms inhabiting riverine environments have become adapted to specific ranges of streamflow. As Fraser

(1972,p.266) points out, "Many [riverine] species have adopted to a rather limited range of velocities or depths of water, and their dependence upon sufficient flow to provide these conditions is complete. " Like most other instream species, anadromous salmonids have adapted their freshwater life history to specific ranges of streamflow parameters. During each stage of salmonids' riverine life history (upstream migration and physical, spawning by adults, incubation of eggs, rearing of juveniles and downstream migration of fry), the viability of fish populations depends on the availability of a distinct, limited set of streamflow conditions.

According to salmonid spawning escapement records for Vancouver Island (Marshall _et_ _al_, 1976; Brown _et_ _al_, 1977; Marshall _et_ _al_, 1977 (a,b); Brown _et_ _al_, 1979 (a,b,c,d); Marshall _et_ _al_, 1980; Department of Fisheries and Oceans, 1985), 34 of the 52 potential SSH peaking power developments on the Island would be located on salmon-producing streams (Figure 3-9). Streamflow alterations due to storage and release of water at SSH facilities may affect the quantity and quality of downstream spawning habitats utilized by Pacific salmon[6]. In order to determine (on both a site-specific and Island-wide basis) the effects of regulated flow regimes on spawning habitats below SSH developments, decision makers must initially identify the relationship between streamflow and spawning habitat availability under natural



(Source: B.C. Hydro, 1981)

FIGURE 3-9. POTENTIAL SSH PEAKING POWER DEVELOPMENTS ON VANCOUVER ISLAND SPAWNING RIVERS.

conditions.

Investigations of Pacific salmon spawning sites indicate substrate composition and streamflow conditions to be the primary factors influencing salmonids' choice of spawning areas (Stalnaker and Arnette,1976; Hamilton, 1978), with stream depth and velocity being most critical to the success of salmonid spawning (Collings,1972; Fraser,1972; Hamilton,1978; Peters,1982; Bottom _et al_, 1985; K. Johansen, pers. comm.,1985).

A spawning bed must be composed of gravel within a suitable size range (gravel sizes between 1.3 and 15.0 cm; Hamilton and Buell,1976) if incubation and subsequent fry emergence are to be successful. Spawning gravel must be free of fine sand, silt or clay to ensure adequate water percolation around the eggs and to provide interstices which allow newly-hatched juveniles to move from the gravel into the stream. On the other hand, gravel must be small enough to enable the female to

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[6] The viability of each freshwater life history stage is important to the subsequent production of adult salmon; however, the potential level of salmonid recruitment is initially determined by the spawning activities of returning adults, which in turn depend on the availability of suitable spawning habitat (Hamilton and Buell, 1976). The remainder of this section will therefore focus on the spawning habitat requirements of Pacific salmon.

excavate a spawning nest or "redd". Substrate composition of spawning areas is to some degree dependent on variations in discharge: periodic peaks in discharge transport gravel from upstream areas to spawning reaches and "flush" fine sediments from spawning bed interstices.

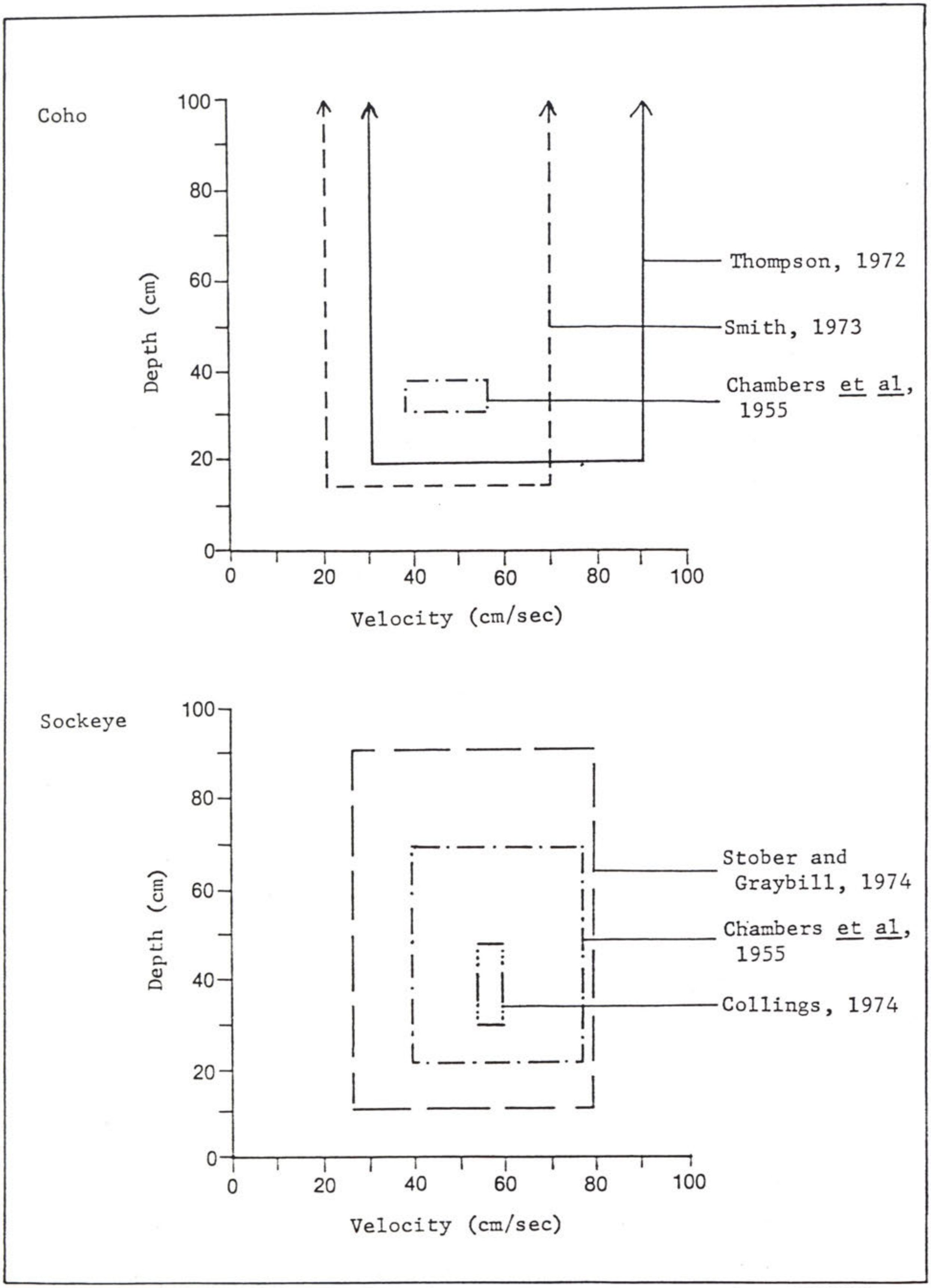
Stream depth appears to be relatively less important than velocity to spawning salmonids. However, minimum depths are required to permit fish movement and reduce the possibility of dessication or predation of deposited eggs. Maximum depths apparently are not a limiting factor since spawning has been observed at depths up to 7m (Newman and Newcombe,1977).

Within an area of suitable spawning gravel, velocity near the riverbed is undoubtedly the most important factor influencing the selection of a spawning site. In the process of spawning, a redd is excavated below the general level of the riverbed by means of a vigorous swatting action of the female's tail. As a result, gravel particles are projected upward where they are caught by the current and moved downstream. Aside from this action, the fish has no physical capability of moving gravel out of its redd. Thus, water velocities adjacent to the streambed must be sufficient to allow successful redd excavation.

Gravel which is carried by the current normally accumulates at the downstream edge of the redd in the shape of a small dune. The presence of this dune induces a low-velocity area or back eddy near the bottom of the redd, thus preventing the newly-deposited eggs from being swept downstream before being covered by gravel from adjacent redd excavation activities. This may be one of the major factors determining the upper velocity limit of spawning salmon, since excessive velocities would move the gravel downstream without allowing a dune to form (Robertson _et al_,1979).

From hydrological measurements in the vicinity of redds, the specific ranges of stream velocity and a minimum depth of water utilized by spawning salmon have been identified (Figures 3-10 through 3-12). The velocity-depth spawning habitat criteria generally suggest that discharge conditions can be a determining factor in the success or failure of spawning activities by salmon (Fraser,1972). However, since natural stream discharge may vary over a period of time, the preferred spawning areas may change with increased or decreased streamflow. Hooper (1973) states that:

> "As flows increase, more and more gravel is covered and becomes suitable for spawning. As flows continue to increase, velocities in some places become too high for spawning, thus cancelling out the benefits of increases in usable spawning area near the edge of the stream. Eventually, as flows increase, the losses begin to outweigh the gains and the actual spawning capacity of the stream starts to decrease," (p.26).



Coho

Sockeye

FIGURE 3-10. REPORTED SPAWNING DEPTH/VELOCITY CRITERIA, COHO AND SOCKEYE SALMON.

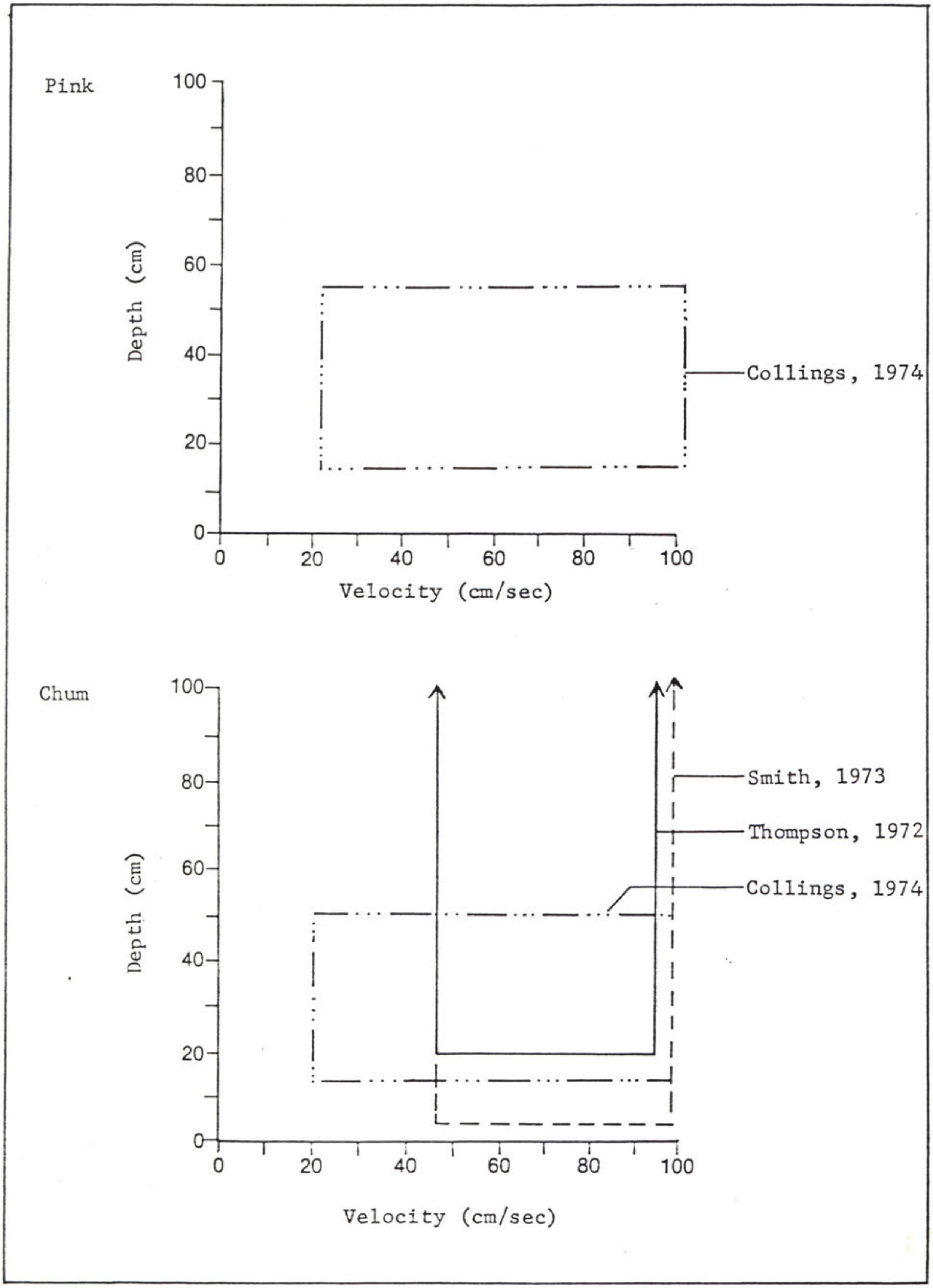


FIGURE 3-11. REPORTED SPAWNING DEPTH/VELOCITY CRITERIA, PINK AND CHUM SALMON.

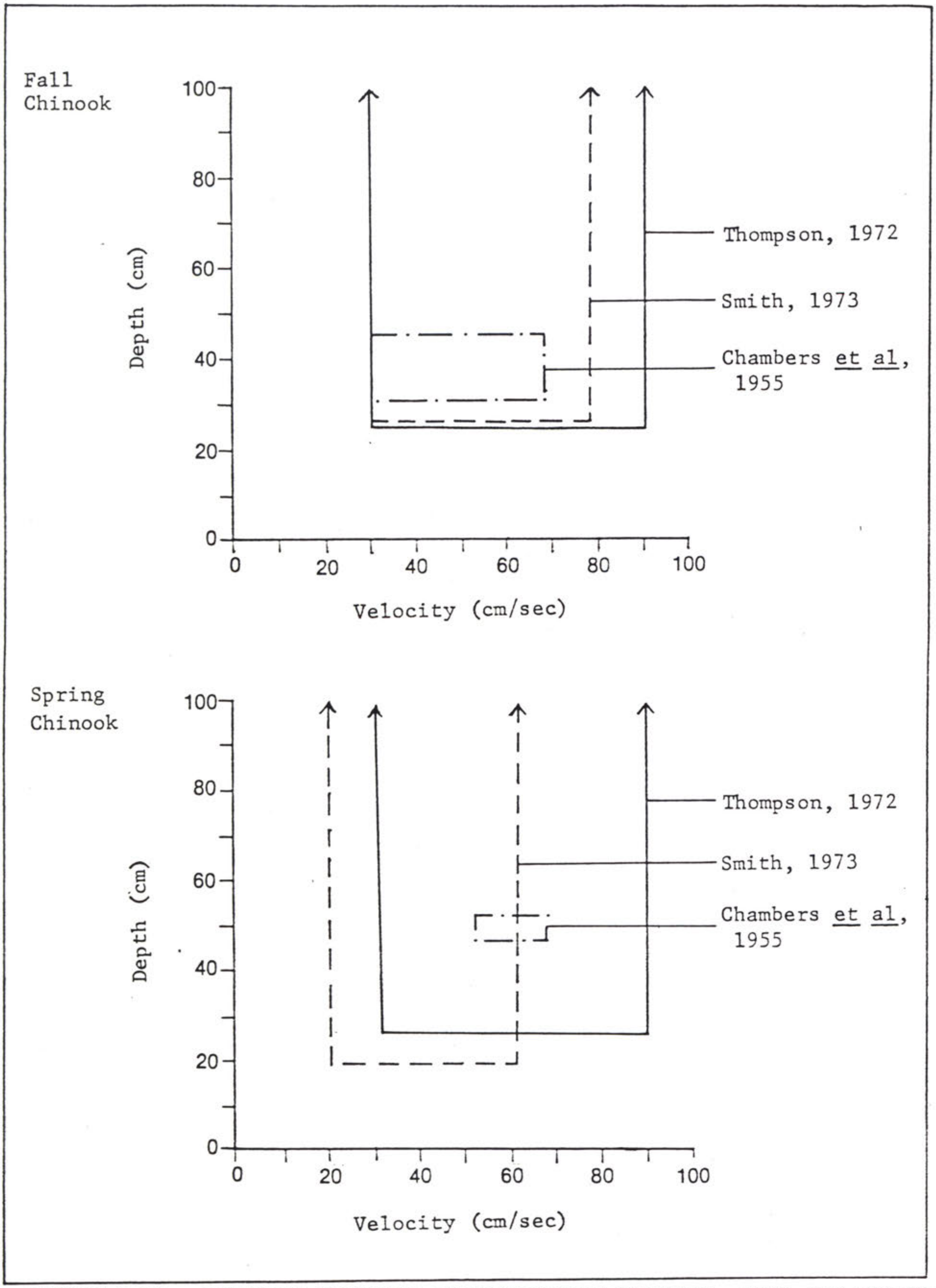


FIGURE 3-12. REPORTED SPAWNING DEPTH/VELOCITY CRITERIA, FALL AND SPRING CHINOOK SALMON.

Conversely, a decrease in discharge may expose floodplain gravels at the margin of the stream, thereby reducing the area suitable for spawning (Berry,1955). Substantial reductions in discharge may reduce water depths and decrease velocities in midstream channels to levels below those required for redd construction. Thus, while stream velocity and depth are the primary determinants of spawning habitat, the actual location and extent of spawning habitat may vary according to both the stream-bed configuration and discharge level. (Fraser,1972).

3.4 Summary

Vancouver Island's mountainous topography and high (if seasonal) annual precipitation provide the necessary generating head and discharge conditions for small scale hydroelectric development at a number of locations. Past inventories of the Island's undeveloped hydro resources have identified 67 sites where head and discharge are sufficient for SSH generating operations. These inventories also indicate that 52 potential SSH sites have storage capabilities which conceivably could allow SSH facilities to operate in a peaking generation mode.

The demand for electricity on Vancouver Island tends to fluctuate regularly over the course of either a day or year. Daily peak loads are usually greatest between 0900 and 2300 hours, while peak seasonal demands tend to occur between the months of October and April. Electrical demand on the Island is currently (and for the immediate future) met to a great extent with power transmitted from the mainland. However, future industrial and/or population growth may lead to peaking power demands which approach the upward limit of Vancouver Island's existing electrical supply. SSH development may be considered as a means of meeting the Island's future peaking power requirements for a number of reasons, including the large amount of peaking power which potentially could be generated at SSH plants, the inherent flexibility in scheduling the development of several small hydro plants as opposed to a single large facility, the ability of SSH facilities to react immediately to changes in electrical demand, and the congruence of seasonal peak loads with periods of greatest discharge on Vancouver Island streams.

Should SSH peaking power facilities be developed on Vancouver Island, significant alterations to downstream flow regimes could result from the configuration of individual SSH plants and water storage and release for power generation at these facilities. Spatial alterations in streamflow may occur between reservoir dams and downstream powerhouses as natural flow is impounded and diverted through a conduit to the powerhouse. Streamflow alterations below SSH facilities may also occur on a daily or seasonal basis. Over a 24-hour period, natural flows may be reduced as water is stored during off-peak hours and enhanced as water is released to generate power during peak load periods; seasonally, streamflow may be impounded during the winter period of high discharge to augment naturally low levels of summer flow.

Pacific salmon have adapted to very specific ranges of spawning bed substrate and stream depth and velocity in spawning areas. Stream velocity appears to be most critical (with minimum stream depth of secondary importance) in determining the quality and quantity of spawning habitat available to Pacific salmon.

The role of streamflow conditions in determining the availability of spawning habitats indicates that spatial and temporal alterations in natural flow regimes could affect the amount and quality of salmonid spawning habitat below SSH facilities. In order for an effective SSH development decision to be made, decision makers must identify the causal relationship between natural streamflow and the quantity and quality of spawning habitat and predict the effects of regulated flow regimes on the availability of such habitats. In the following chapter, data concerning discharge-spawning habitat relationships in selected Vancouver Island streams are reviewed to determine the quality of information (ranging from wholly functional to wholly descriptive) which is currently available to decision makers. The quality of available information is then assessed to ascertain whether a decision to allocate stream flow for SSH peaking power developments could be made under conditions of certainty, risk or uncertainty with respect to the possible effects of that allocation on salmonid spawning habitat.

CHAPTER 4

INFORMATION QUALITY AND UNCERTAINTY REGARDING SMALL SCALE HYDROELECTRIC DEVELOPMENTS ON VANCOUVER ISLAND SPAWNING STREAMS

4.1 Introduction

To enhance the generating efficiency of individual SSH peaking power facilities, water must be stored and released on both a daily and seasonal basis. These periods of storage and release will necessarily result in the modification of natural discharge conditions below SSH developments. Since the quantity and quality of salmonid spawning habitat in a stream reach is dependent (assuming a suitable substrate is present) on the velocity and depth of streamflow, changes in natural flow conditions may affect the quantity and quality of spawning habitat in reaches below SSH developments. Although the magnitude of changes to spawning habitats vary according to site-specific characteristics of the SSH development, these changes tend to be relatively minor compared with those associated with larger hydro facilities. However, several SSH developments within a circumscribed region may substantially change the overall quantity and quality of spawning habitats in that area (Loar and Sale,1981). To ensure that an effective SSH development decision is made, decision makers must predict the changes to spawning habitats (on both a river-specific and Island-wide basis) arising from flow alterations below SSH developments.

A decision to allocate streamflow for SSH peaking power plants on Vancouver Island streams may be made under conditions of certainty, risk or uncertainty according to the ability (or inability) of decision makers to predict the effects of flow alterations on downstream spawning habitats. The conditions under which the allocative decision is made would depend on the quality of information available to decision makers regarding the influence of various discharge levels on spawning habitat quantity and quality. If a complete set of functional information specifying a causal relationship between discharge and spawning habitat conditions is available to decision makers, the amount or quality of spawning habitat associated with various discharge conditions can be predicted. In addition, the availability of such data allows accurate predictions of changes to downstream spawning habitats caused by flow alterations below SSH peaking facilities. In this situation, a decision regarding the possible development of Vancouver Island's peaking power potential will be made under conditions of certainty. If the available information is primarily functional in nature, probabilistic estimates of changes in downstream spawning habitats can be derived and the subsequent allocative decision will be made under conditions of risk. However, if the existing data is primarily or completely descriptive in nature, accurate predictions or probabilistic estimates of effects on downstream spawning habitats cannot be derived. In this case, a decision concerning the development of SSH peaking facilities on Vancouver Island spawning streams will be made under conditions of uncertainty.

This chapter examines existing information regarding the discharge-spawning habitat relationship in selected Vancouver Island rivers. The intent of the following analysis is two-fold: 1) to determine the descriptive or functional nature of existing information outlining the discharge-spawning habitat relationship within selected Vancouver Island rivers, and 2) to ascertain whether the quality of existing information will cause a decision regarding streamflow allocations for SSH peaking power developments on Vancouver Island spawning streams to be made under conditions of uncertainty.

4.2 Characteristics of Study Rivers

4.2.1. Utilization of Study Rivers by Spawning Salmon

Twenty-two of the 52 Vancouver Island rivers with undeveloped SSH peaking power sites are presently utilized by spawning salmon (Table 4-1). To compile and assess the quality of all information concerning discharge and spawning habitat conditions in the twenty-two rivers was not possible given time and logistic constraints. Five rivers (the Burman, Nahmint, Nimpkish, Sarita and White Rivers) were randomly chosen to serve as the focii of the subsequent information quality analysis (Figure 4-1).

Headwaters of the Burman, Nahmint and Sarita Rivers originate in the western highlands of the Vancouver Island Mountains, while the Nimpkish and White rivers begin in mountainous regions to the east of the divide. Streamflow in all of the rivers is unregulated.

The Sarita River watershed has a drainage area of 162 km^2 and flows to Numukanis Bay on the Island's west coast. Sarita Lake, the only major storage basin in the system, is located approximately 10 km from the river mouth. During the past fifteen years, maximum annual spawning escapements of about 73,000 salmon have been recorded for the Sarita River, with chum salmon as the most numerous species. Smaller numbers of chinook and coho spawn in this system, while intermittent runs of sockeye and pink salmon have also been reported. Spawning by chinook, coho and chum occurs throughout the Sarita River up to an impassable waterfall located 9.7 km from the river mouth.

The Burman River drains a watershed of 259 km^2 and empties into Muchalat Inlet on the west coast. Several lakes empty into the Burman, the largest of which (Burman

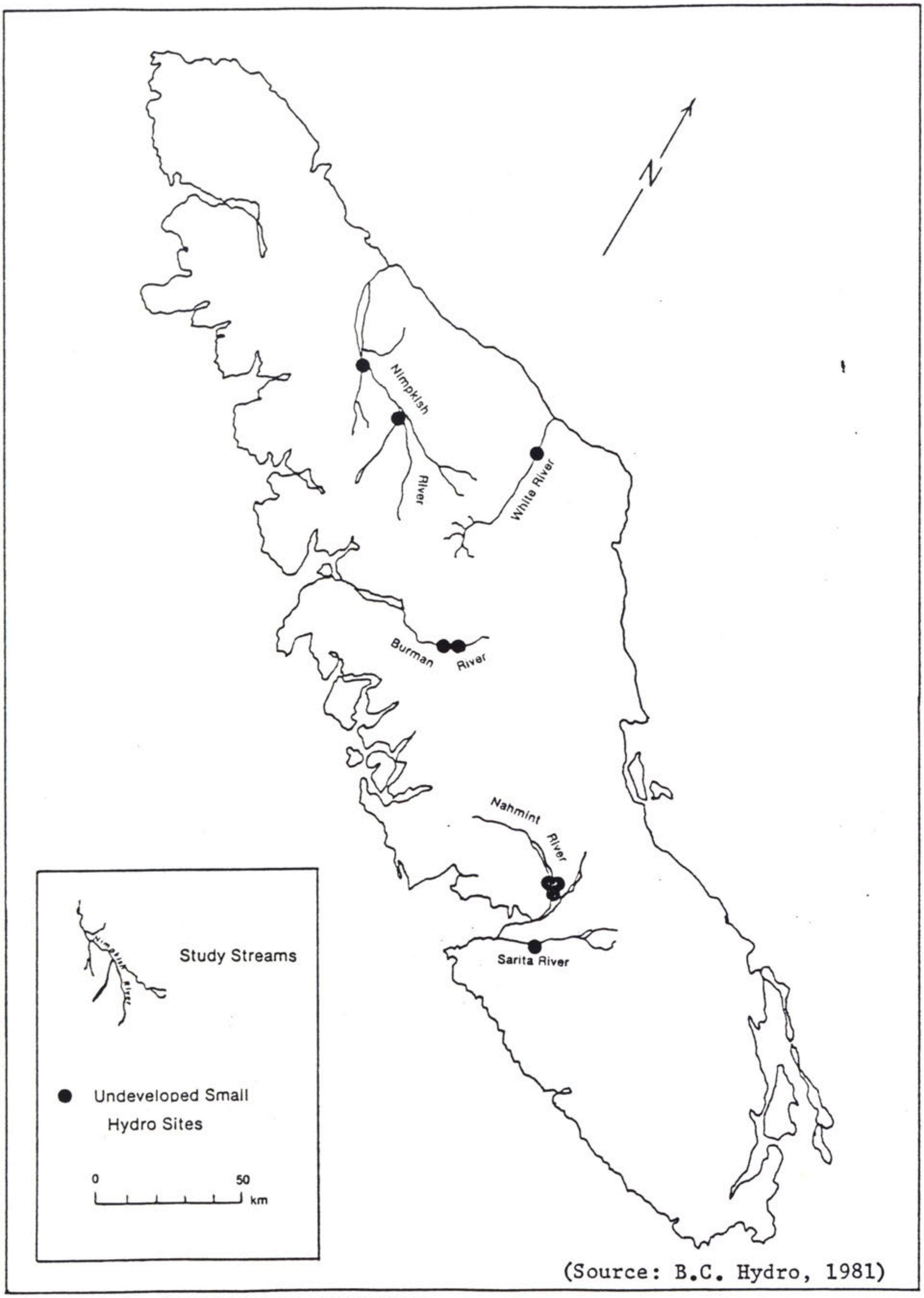
TABLE 4-1. POTENTIAL SSH PEAKING POWER DEVELOPMENTS LOCATED ON VANCOUVER ISLAND SPAWNING STREAMS.

SPAWNING STREAM	SSH SITE NAME(S)
BENSON RIVER	BENSON RIVER
BURMAN RIVER	NORTH FORK SITE 2
CONUMA RIVER	CONUMA RIVER
COWICHAN RIVER	MARIE CANYON
DRINKWATER CREEK	DRINKWATER FALLS
LITTLE QUALICUM RIVER	LITTLE QUALICUM FALLS CAMERON LAKE
MAHATTA CREEK	MAHATTA CREEK
MARBLE RIVER	VICTORIA LAKE MARBLE CANYON AMAZON FALLS
NAHMINT RIVER	DIVERSION "L" DIVERSION "M"
NANAIMO RIVER	BEAR DEN CANYON NANAIMO DIVERSION SITE 1 NANAIMO DIVERSION SITE 2 NANAIMO DIVERSION SITE 3 NANAIMO LAKES
NIMPKISH RIVER	CAMOUSON CANYON BIG FALLS
QUALICUM RIVER	QUALICUM RIVER (LINE M) QUALICUM RIVER (LINE L)

TABLE 4-1 (continued)

RAGING RIVER	MAYNARD LAKE
SARITA RIVER	SARITA FALLS
SHAWNIGAN CREEK	SHAWNIGAN LAKE
SOMASS RIVER	SOMASS FALLS
SPROAT RIVER	SPROAT FALLS
STAMP RIVER	LOWER STAMP FALLS UPPER STAMP FALLS
TAHSISH RIVER	TAHSISH RIVER
TSABLE RIVER	TSABLE RIVER
WHITE RIVER	WHITE RIVER
ZEBALLOS RIVER	ZEBALLOS RIVER

SOURCE: BRITISH COLUMBIA HYDRO AND POWER AUTHORITY, 1981.



(Source: B.C. Hydro, 1981)

FIGURE 4-1. STUDY RIVER LOCATIONS.

Lake) is located 30 km from the river mouth. Annual escapements of up to 168,000 salmon have been recorded since 1970, the majority of which tend to be pink salmon. A secondary population of chum spawn in Burman River while small numbers of sockeye, chinook and coho also utilize the river. Most spawning activity occurs in the lower 5 km of the river although some spawning has occurred up to 8 km from the mouth.

The Nahmint River drains an area of 140 km^2 and flows into Alberni Inlet. Nahmint Lake, the major storage basin in the Nahmint system, is situated about 12.5 km from the mouth of the river. Since 1970, up to 41,000 spawners have been counted with chum salmon being the most numerous species. Relatively small stocks of pink, sockeye, chinook and coho also spawn in this river. Spawning by all species tends to occur throughout the river up to a set of impassable falls located 4.8 km from the mouth.

On the eastern side of Vancouver Island, the White River drains an area of 337 km^2 and runs southeast to its confluence with the Salmon River. No escapement figures are available for the White River; however, pink salmon, chinook, coho, and sockeye are known to spawn in the river. Chinook spawning activites have been recorded to a point 5 km above the junction with the Salmon River, while the remaining species spawn throughout the White River.

Finally, the Nimpkish River drains a watershed of about 1760 km^2 and flows into Broughton Strait. Nimpkish and Woss Lakes are the major storage basins for the system. The Nimpkish River supports more spawning activity than any of the other study rivers, with recorded annual escapements of up to 179,000 fish since 1970. Sockeye dominate escapements into the river, with smaller populations of chum and very limited numbers of chinook, coho and pink also spawning in the river. Sockeye, chinook and coho spawn throughout the Nimpkish River system while chum and pink salmon tend to spawn below Nimpkish Lake.

4.2.2 Spawning Reaches Potentially Affected by SSH Developments

Eight undeveloped sites on the study rivers have been identified as suitable for SSH peaking power generating facilities (B.C. Hydro, 1981). According to proposed project designs outlined by B.C. Hydro for each site, only the spawning habitat in the White River may be affected by a spatial alteration in streamflow. The conceptual design of the White River SSH development anticipates diversion of water from a series of small, upstream dams through a 3 km penstock to the powerhouse, which would be located 4 km upstream of the White-Salmon confluence. Such a diversion could alter the velocity and depth of flows between the diversion dams and powerhouse, possibly affecting spawning habitat used by chinook, coho and pink salmon.

While diversion of water may affect up to 3 km of the spawning area in the White River, a larger proportion of the spawning reaches in all five study rivers may be affected by modified patterns of daily and seasonal discharge below SSH generating plants. At all eight SSH sites on the study rivers, water would be impounded and released over a 24-hour period to generate power for daily peak load requirements. Large and very rapid fluctuations in discharge would therefore be evident downstream of the powerhouses over the course of each day. On the Burman, Nahmint and Sarita Rivers, water would be stored in dammed upstream lakes during the fall and winter months and slowly released over the course of the following summer. On these rivers, seasonal alterations to natural flow patterns would be observed below SSH facilities in addition to short-term fluctuations caused by daily storage and release of water.

Daily and seasonal alterations in natural flow patterns may affect a significant proportion of the spawning reaches in each study river. Virtually all spawning areas in the Burman, Nahmint and Sarita Rivers could be subjected to low flows during the fall and winter months as water is impounded in upstream lakes. Spawning beds in the lower 4 km of the White River, the lower 35 km of the Nimpkish River, and throughout the Burman, Nahmint and Sarita rivers may experience rapid changes in stream velocity and depth as water is impounded and released in concert with daily peaking power requirements.

4.3 Information Quality and Uncertainty Associated With Existing Discharge and Spawning Habitat Data

4.3.1. Information Quality Assessment Scheme

Despite the large body of decision making literature concerned with information and uncertainty in decision situations, objective measures of information quality have not been forthcoming. A somewhat subjective scheme was thus devised to assess the quality of data regarding discharge and spawning habitat conditions in each study river. The resulting analytical framework is essentially comprised of two linked components. The first component consists of a hierarchy of five information levels, each successive level of data increasingly specifying spawning habitat conditions as a function of stream discharge levels. The second component consists of the estimated quality of information in each level (using the "descriptive-functional" spectrum of information quality proposed by Dorcey and Hall (1981)). These five levels of data and the estimated quality of information in each level provide a basis for classifying and assessing the discharge and spawning habitat information available for the five study rivers.

Several steps were required to produce the assessment scheme. First, the range of discharge and spawning habitat data which might be available during the hypothetical SSH decision process was identified. The availability of such data presupposes some form of on-site biophysical inspection and/or measurement; for that reason, the range of potentially-available data was identified from the output data of existing spawning habitat evaluation methodologies. Four basic categories of information were distinguished by this review. These ranged from a general description of discharge levels and spawning bed locations to a precise quantification of the quality and quantity of spawning habitat directly associated with varying discharge conditions (Table 4-2). A fifth category (designated "no information") was included to account for the possibility that stream-specific discharge and spawning habitat data may be completely unavailable during the decision process.

Having identified the range of potentially-available information, the relative degree to which each class of data specified a causal relationship between discharge and spawning habitat conditions was determined. Salmon habitat management personnel (K. Johansen, A. Stefanson, B. Tutty) were asked to appraise the relative extent to which a causal relationship between discharge levels and spawning habitat conditions was defined by information in each of the five categories. The appraisals were

TABLE 4-2. DISCHARGE AND SPAWNING HABITAT DATA POTENTIALLY AVAILABLE THROUGH THE USE OF EXISTING SPAWNING HABITAT ASSESSMENT METHODS.

ASSESSMENT DATA CHARACTERISTICS	ASSESSMENT METHOD	REFERENCES
Historical records of discharge levels; spawning beds located and mapped	Field Observation Aerial Reconnaissance Hydrological Measurements	Fielden, 1971 Bond *et al*, 1975 Moore, 1977 Brown *et al*, 1979 Kapahi, 1983
Quantity and quality of spawning habitat evaluated as a function of one discharge condition	Oregon Fish Commission Method Rantz Method Idaho Method	Sams and Pearson, 1963 Rantz, 1964 Idaho Water Resources Board, 1969
Quantity and quality of spawning habitat evaluated as a function of more than one but less than all possible discharge conditions	Planimetric Mapping Oregon Game Commission Method Weighted Usable Area Method	Collings, 1972; 1974 Thompson, 1972 Newcombe, 1981
Quantity and quality of spawning habitat evaluated for all possible discharge conditions	Physical Habitat Simulation (PHABSIM) Modelling	Stalnaker, 1979 Trihey, 1979 Loar and Sale, 1981
No information available regarding discharge or spawning habitat conditions	----------------------	--------------------

completely consistent, not surprisingly indicating that a causal relationship between discharge and spawning habitat is specified least by unconnected measurements of discharge and spawning habitat and is best defined by concurrent measurement of all discharge levels and the habitat conditions associated with those discharges. On the basis of those appraisals, the five categories were arranged as a hierarchy with each successive level reflecting a relatively greater specification of the discharge-spawning habitat relationship (Table 4-3).

Finally, the relative functional or descriptive nature of the information in each level was estimated. In Dorcey and Hall's (1981) view of information quality, the descriptive or functional nature of information is dependent upon the degree to which the data expresses a causal relationship between elements of the system under consideration. Accordingly, information which was previously appraised as leaving the discharge-spawning habitat relationship completely unspecified (Level II data in Table 4-3) can be seen as "totally descriptive" in nature; the quality of Level V data, which completely specifies a causal relationship, can be viewed as "wholly functional" (Table 4-4). Level III information outlines the quality and quantity of spawning habitat associated with a single discharge level, but no relationship can be discerned from this level of data. Thus, the quality of Level III information can be rated as "primarily

TABLE 4-3. APPRAISED SPECIFICATION OF DISCHARGE-SPAWNING HABITAT RELATIONSHIPS BY CATEGORIES OF SPAWNING HABITAT ASSESSMENT DATA.

	ASSESSMENT DATA CHARACTERISTICS	APPRAISED SPECIFICATION OF DISCHARGE-SPAWNING HABITAT RELATIONSHIP
I.	No information available regarding discharge or spawning habitat conditions	Any consideration of a relationship between discharge and spawning habitat conditions is rendered meaningless by the complete lack of data
II.	Historical records of discharge levels; spawning beds located and mapped	Causal relationship between discharge and spawning habitat conditions is not specified by this data
III.	Quantity and quality of spawning habitat evaluated as a function of one discharge condition	Causal relationship between discharge and spawning habitat conditions is not specified by this data
IV.	Quantity and quality of spawning habitat evaluated as a function of more than one but less than all possible discharge conditions	Causal relationship between discharge and spawning habitat conditions is specified only for the measured range of discharge; overall relationship may be estimated from this information
V.	Quantity and quality of spawning habitat evaluated for all possible discharge conditions	Causal relationship between discharge and spawning habitat conditions is completely specified by this data

Sources: K. Johansen, A. Stefanson, B. Tutty, personal communications, 1985.

TABLE 4-4. ESTIMATED QUALITY OF SPAWNING HABITAT ASSESSMENT DATA.

	ASSESSMENT DATA CHARACTERISTICS	ESTIMATED QUALITY OF ASSESSMENT DATA
I.	No information available regarding discharge or spawning habitat conditions	Information quality cannot be assessed
II.	Historical records of discharge levels; spawning beds located and mapped	Completely descriptive in quality
III.	Quantity and quality of spawning habitat evaluated as a function of one discharge condition	Primarily descriptive in quality
IV.	Quantity and quality of spawning habitat evaluated as a function of more than one but less than all possible discharge conditions	Primarily functional in quality
V.	Quantity and quality of spawning habitat evaluated for all possible discharge conditions	Completely functional in quality

Adapted from Dorcey and Hall, 1981

descriptive". Level IV information outlines the habitat conditions associated with several discharge levels, but does not contain sufficient measurements to render the discharge-spawning habitat relationship absolutely predictable. Instead this level of data only allows probabilistic estimates of the habitat conditions associated with varying levels of discharge. Therefore, Level IV data can be seen as "primarily functional" in quality. Since Level I indicates a complete lack of data, no estimate of information quality can be made.

4.3.2 Compilation of Discharge and Spawning Habitat Information for the Study Rivers.

A comprehensive compilation of literature pertaining to biophysical conditions and fisheries resources in the five study rivers was undertaken. Information sources included field reports, aerial surveys, and biophysical reconnaissances carried out by the Department of Fisheries and Oceans (DFO), the British Columbia Fish and Wildlife Branch, and independent consultants. These were supplemented with information provided by DFO fisheries officers and technicians responsible for on-site inspections and management of salmon habitat in the study rivers. Some information was also provided by personal interviews with B.C. Fish and Wildlife biologists.

4.3.3 Quality of Existing Discharge and Spawning Habitat Information

On the basis of personal interviews with fisheries habitat management personnel and the review of biophysical data, it became evident that spawning habitat conditions have not been measured in conjunction with discharge levels in the study rivers. Instead, the available data is restricted to historical discharge records and mapped locations of spawning beds (Table 4-5).

Referring to the hierarchy of information levels in Table 4-2, it can be seen that existing discharge and spawning habitat information for the study rivers can be classed as Level II data. Level II information does not specify any causal relationship between discharge and spawning habitat conditions; instead, discharge and spawning habitats are examined as unrelated entities. Thus, according to Dorcey and Hall's (1981) conception of information quality, this level of data can be characterized as "wholly descriptive" in nature (Table 4-4).

4.3.4 Uncertainty Associated With Existing Discharge and Spawning Habitat Data

Information viewed as wholly descriptive in quality is characterized by measurements or descriptions of

TABLE 4-5. SUMMARY OF EXISTING DISCHARGE AND SPAWNING HABITAT INFORMATION FOR THE BURMAN, NAHMINT, NIMPKISH, SARITA AND WHITE RIVERS.

STUDY RIVER	CHARACTERISTICS OF AVAILABLE INFORMATION	SOURCES
Burman River	Historical records of discharge levels	Environment Canada, 1983
	Mapped locations of spawning beds	D. Girodat, personal communication, 1985
Nahmint River	Historical records of discharge levels	Environment Canada, 1983
	Mapped locations of spawning beds	Wilson and Rapp, 1971 Burns and Hazeldine, 1973 Bond et al, 1975 Cameron and Fuchs, 1975 D. McCulloch, personal communication, 1985
Nimpkish River	Historical records of discharge levels	Environment Canada, 1983
	Mapped locations of spawning beds	Gould and Stefanson, 1985 J. Lewis, personal communication, 1985

TABLE 4-5. (continued)

Sarita River	Historical records of discharge levels	Environment Canada, 1983
	Mapped locations of spawning beds	Frederick and Harding, 1971 D. McCulloch, personal communication, 1985
White River	Historical records of discharge levels	Environment Canada, 1983
	Mapped locations of spawning beds	Harding and Burns, 1971 J. Trent, personal communication, 1985

distinct parts or elements of the system under study rather than a specification of relationships between those elements (Dorcey and Hall, 1981). The availability of descriptive information does not allow decision makers to identify or predict the direct and indirect consequences of actions arising from implementation of a decision on all elements and processes comprising the potentially-affected system. In the context of this analysis, the existing data does not specify a causal relationship between varying discharge levels and spawning habitat conditions in the study rivers. For that reason, decision makers cannot predict (or even estimate in a probabilistic sense) the effects of daily and/or seasonal flow alterations on the quantity and quality of spawning habitats below SSH facilities on these rivers. According to decision theorists, conditions of uncertainty exist in a decision situation when the specific or probable outcomes of a selected course of action are unknown (March and Simon, 1959; Richards and Greenlaw, 1972; Bridge and Dodds, 1975; Anderson, 1982). Given the inability of decision makers to predict or estimate the effects of flow alterations on downstream spawning habitats, it would appear that conditions of uncertainty would be present in a decision situation involving SSH peaking power developments on the study rivers.

The uncertainty associated with SSH developments on the study rivers may extend to a broader decision situation, namely the potential development of all SSH sites located on Vancouver Island spawning streams. Existing discharge and spawning habitat data for the study rivers (consisting solely of historical discharge records and mapped locations of spawning beds) is apparently representative of the total discharge and spawning habitat data available for the majority of Vancouver Island spawning streams (J. Lewis, D. McCulloch. A. Stefanson, B. Tutty, pers. comms., 1985). Assuming this is the case, the existing data for the majority of Island spawning streams would not specify a causal relationship between discharge and spawning habitat conditions, and thus, the quality of such data could be classed as "wholly descriptive". Decision makers using such descriptive information therefore cannot predict or estimate the stream-specific (for most rivers) or Island-wide effects of altered flows on spawning habitats below SSH peaking facilities. Thus, conditions of uncertainty would appear to be present in any decision situation involving the possible development of SSH sites located on Vancouver Island salmon spawning streams.

4.4 Summary

Development of Vancouver Island's SSH potential on rivers utilized by spawning salmon may lead to significant changes in the quantity and quality of spawning habitat on the Island. An effective decision concerning such development, therefore, requires a full understanding by decision makers of the possible river-specific and Island-wide effects of water storage and release on downstream spawning habitats.

A decision regarding SSH developments on spawning streams may be made under conditions of certainty, risk or uncertainty with respect to the possible effects of streamflow alterations on spawning habitats below SSH facilities. The conditions under which a decision is made depends on the information available to decision makers concerning the relationship between discharge and spawning habitat conditions in potentially-affected streams. An assessment of existing discharge and spawning habitat information for selected Vancouver Island rivers was therefore undertaken to: a) determine the descriptive or functional nature of that data, and b) ascertain whether the quality of existing information will foster conditions of uncertainty in a decision situation involving SSH developments on Vancouver Island salmon spawning rivers.

From the twenty-two rivers and streams identified as providing impoundment capabilities for SSH peaking facilities and spawning areas for Pacific salmon, five (the Burman, Nahmint, Nimpkish, Sarita and White rivers) were randomly selected to serve as the focii of the information quality assessment.

An assessment scheme was devised to analyze the quality of existing discharge and spawning habitat information for the study rivers. The scheme consists of two linked components: 1) a hierarchy of five information categories, each level increasingly specifying the spawning habitat condition associated with varying discharge levels, and 2) the estimated quality of information in each level based on the degree to which individual levels of data specify a causal relationship between discharge and spawning habitat conditions.

Existing discharge and spawning habitat information for the study rivers was compiled from biophysical reconnaissance reports supplemented with personal communication with D.F.O. and B.C. Fish and Wildlife personnel. Available data for all study rivers was found to consist solely of daily discharge records and the locations of spawning beds in each river. Information for each study river was judged to be "wholly descriptive" in quality.

Decision makers using this descriptive data cannot predict or estimate the possible effects of SSH developments on downstream spawning habitats in the study rivers. Thus, conditions of uncertainty would be evident in a decision situation involving possible SSH peaking power developments on the selected study rivers. The discharge and spawning data compiled for the study rivers are apparently representative (in terms of the degree to which the available data specifies the relationship between discharge and spawning habitat conditions) of similar information for the majority of Vancouver Island spawning streams. Assuming this is the case, the available discharge and spawning habitat information for the majority of Vancouver Island spawning streams would also be classed as "wholly descriptive" in quality. Therefore, conditions of uncertainty would also be present in a decision situation involving Island-wide development of SSH sites on spawning rivers.

CHAPTER 5

STUDY LIMITATIONS, IMPLICATIONS AND CONCLUSIONS

5.1 Study Limitations

In formulating the assessment scheme, two problems were encountered which may affect the results of this and future information quality analyses. The first problem lies with the limited number of salmon habitat management personnel who provided estimates of the degree to which a causal discharge-spawning habitat relationship was expressed by data in the five information categories (Table 4-3). While these estimates were entirely consistent within the response group, they may not represent the perceptions of other salmon habitat managers or managers of non-fishery resources. These estimates (and the assigned qualities of information derived from these estimates) may be biased to some degree. Thus, it must be recognized that the appraised quality of actual data (according to the assessment framework) may similarly be biased, although there is no objective standard by which the magnitude and direction of possible bias can be measured.

A second problem originates with the

conceptualization of information quality. The conceptual basis for estimates of information quality within the assessment scheme lies with Dorcey and Hall's (1981) view of data quality as a spectrum ranging from "wholly descriptive" to "wholly functional" information. The extremes of this spectrum are relatively well defined: there is little difficulty in distinguishing information of "wholly descriptive" or "wholly functional" quality from data of intermediate qualities. However, the division between "primarily descriptive" and "primarily functional" qualities is not as apparent. It is not clear from Dorcey and Hall's concept how the relative proportions of descriptive and functional information can be determined when examining a body of data. There are no empirical means of determining how much of the data set is comprised of functional or descriptive information, or what quantity of systemic information is needed to transform a "primarily descriptive" set of data to one which is "primarily functional" in quality. Thus, it must be re-emphasized that the data qualities assigned to Levels III and IV information in the analytical framework are simply <u>approximations</u> and are not definitive in character. Although not affecting the results of this analysis, some care should be taken in future analyses using this framework when characterizing actual data as either "primarily descriptive" or "primarily functional" in quality.

5.2 Discussion and Recommendations

The preceding analysis found existing discharge and spawning habitat data for the study rivers to be wholly descriptive in quality. Based on this information, a decision to develop SSH peaking power facilities on the study rivers would be made under conditions of uncertainty with respect to possible effects on downstream spawning habitats. Since flow and spawning habitat data for the majority of Vancouver Island spawning streams is evidently descriptive in quality, it would seem that decisions involving SSH developments on Island spawning streams would generally be made under conditions of uncertainty.

The uncertainty associated with the descriptive quality of existing data will affect future SSH development decisions in a number of ways. First, decision makers' efforts to mitigate potential effects of peaking SSH facilities on downstream spawning areas will be inhibited. To determine the design or operational changes needed to alleviate possible effects on spawning habitats, decision makers must accurately assess the potential impacts on these habitats from SSH developments. As previously indicated, causal linkages between discharge and spawning habitat conditions cannot be determined from the existing descriptive data; for that reason, the types and magnitude of possible impacts can neither be predicted nor accurately estimated. Consequently, decision makers cannot objectively determine which modifications in SSH facilities' design or operations would effectively reduce or avoid changes to downstream spawning habitats.

Second, uncertainty will restrict the ability of decision makers to enhance existing spawning habitats by means of storage and release of water at SSH facilities. Spawning habitat quality or quantity in unregulated streams may be limited by excessive or insufficient flows during spawning periods. If the discharge-spawning habitat relationship in these streams can be determined, the magnitude and timing of streamflow storage and release at SSH plants can be planned to cause a net increase in usable spawning areas. Unfortunately, the effects of streamflow regulation cannot be predicted from existing discharge and spawning habitat information, and thus, habitat enhancement opportunities may be precluded.

Third, and most important, attempts by decision makers to subjectively reduce uncertainty in SSH decision situations will introduce biases into assessments of SSH developments' effects on downstream spawning habitats. Decision makers may respond to uncertainty in the SSH decision by avoiding the act of decision, by restricting the scope of the decision process to factors other than possible impacts to spawning habitats, or by forming subjective estimates of decision consequences in order to reduce the uncertainty. It is not likely that the first two responses will be employed for the following reasons:

a) once the need for peaking power is identified, a decision to allocate streamflow for SSH developments <u>must</u> be made within a specified time period in order that sufficient "lead time" is available for planning and construction of SSH facilities, and b) the high profile and strong public and government support for salmon habitat conservation activities will force decision makers to examine potential impacts to salmon habitats in SSH decision processes. Instead, decision makers will most probably opt to "reduce" the uncertainty by estimating the effects of various allocation strategies on downstream spawning habitats. Since there are no objective bases from which the effects of flow alterations below SSH facilities can be determined, decision makers will be forced to rely on past experiences and "professional judgements" to identify the types and magnitudes of possible changes to spawning habitats. The accuracy of these estimated effects obviously depend upon the depth and breadth of decision makers' training or experience. In addition, the nature and extent of the consequences identified by decision makers may reflect the political, bureaucratic or personal biases or goals of the decision group. For these reasons, it is unlikely that decision makers will accurately assess the consequences of proposed flow allocations for SSH developments.

Ultimately, the uncertainty associated with existing discharge and spawning habitat data will lead to ineffective streamflow allocations. As outlined earlier in this thesis, the effectiveness of a resource allocation (the degree to which desired outcomes are achieved) is dependent on a) the decision maker's understanding of interrelationships between a proposed resource use and the social or ecological systems which may be affected, and b) his ability to predict the consequences of a particular allocation strategy. The possible change in the character of the resource base (alteration of natural flow regimes) and the potential consequences of that change (increase or decrease in the quality and quantity of downstream salmon spawning habitats) can be readily identified. However, it is also clear from the preceding discussion that the magnitude and types of potential changes to spawning habitats below SSH facilities can neither be predicted nor accurately estimated. The uncertainty surrounding the possible consequences of SSH development and the probability of biased assessments of streamflow allocation strategies increase the likelihood of unanticipated or negative decision outcomes. It is unlikely that such a decision will maximize the benefits of SSH developments and minimize or avoid deleterious impacts on spawning habitats. Indeed, under conditions of uncertainty, a truly effective streamflow allocation would be made by chance rather than by rational choice. Thus, from the preceding information quality analysis and discussion, it would appear that the research argument expressed in

Chapter 1 has been borne out.

As a final observation, it should be noted that the uncertainty associated with alterations in spawning stream flows will not be restricted to SSH development decisions. Future industrial, municipal or domestic developments on Vancouver Island may require water to be diverted or withdrawn from spawning streams. The consequent alterations in discharge, while spatially and temporally dissimilar from those caused by SSH developments, may affect spawning habitats below the points of flow diversions or withdrawals. Assuming that the existing quality of discharge and spawning habitat information does not change, decision makers will not be able to predict or estimate the consequences of these flow alterations, just as the effects of modified flows below SSH facilities cannot be estimated or predicted. Thus, conditions of uncertainty (and the possibility of an ineffective flow allocation) will be present in <u>any</u> decision situation where proposed alterations of streamflow may affect downstream spawning habitats.

Several recommendations can be derived from this analysis. First, decision makers must be made aware of the link between the quality of available information and uncertainty reduction in resource allocation decisions. Decision makers (and many decision theorists) have tended to regard uncertainty as a condition arising from <u>quantitative</u> deficiencies in data. Where this view is held, the reduction or elimination of uncertainty in a decision situation is achieved simply by acquiring additional information concerning the elements of systems potentially affected by the decision. As this thesis has demonstrated, however, uncertainty stems from qualitative deficiencies in available information. Therefore, decision makers can only reduce or eliminate uncertainty by acquiring a specific kind of information, namely that data which outlines causal linkages between elements of potentially-affected systems.

Second, decision makers must understand that ineffective resource allocations are the likely product of attempts to subjectively reduce uncertainty. Decision theorists have shown that subjective estimates of decision results may be inaccurate and biased and thus, an allocative decision will in all liklihood be ineffective in maximising resource development benefits while minimising or avoiding deleterious impacts on existing or future resource uses. To ensure that future resource allocations are indeed effective, decision makers must reduce uncertainty by objective means, specifically by increasing the predictability of potentially-affected systems through aquisition of functional information.

Finally, the results of this study indicate a need for decision makers to anticipate functional data requirements in order to forestall uncertainty in future resource allocation decisions. Many decision makers operate in a "reactive" manner with respect to the acquisition of functional data concerning the biophysical bases of resource uses. Because of the large expenditures of time and money required to collect such data, functional information is not usually acquired until a specific resource development is proposed (B. Tutty, pers. comm., 1985). Unfortunately, by delaying research activities until after the onset of the resource allocation decision process, decision makers may not be able to reduce uncertainty to the fullest possible extent. Once the resource development is formally proposed and the decision process is underway, decision makers must compile existing data regarding the biophysical bases of existing and future resource uses, identify data gaps causing uncertainty, assign priorities for research, and collect the information needed to predict or accurately estimate the effects of alternative resource allocations, all within a very limited period of time. Given the time required for the preliminary stages of data collection and the multiple, detailed measurements needed to establish causal relationships between elements of systems under consideration, it may not be possible to collect the required functional data within the time frame allotted for the allocative decision. Thus, a reactive strategy of functional data acquisition may actually restrict decision makers' ability to reduce or eliminate uncertainty once the decision process is underway.

A logical alternative might be some form of "anticipatory" approach to data acquisition, wherein an advance review is undertaken to identify a) the most suitable locations for specific types of resource developments, b) the biophysical systems which may be affected by these developments, c) the functional data needed to avoid uncertainty in future allocative decision processes. Through the use of such an approach, decision makers could at the very least begin data collection activities upon the start of a resource decision process, having already determined the information required for an effective allocation decision. Perhaps more important, decision makers who identify future data needs have the opportunity to acquire the necessary functional data <u>in advance</u> of the decision process, thereby allowing accurate predictions of impacts to be derived from the conceptual designs of proposed resource developments.

In closing, the analysis undertaken in this thesis explored the linkages between information quality, uncertainty and decision effectiveness, and revealed the inadequacy of descriptive data for objective, rational resource allocation decisions. The effectiveness of future resource decisions can be increased by decision makers' efforts to objectively reduce or avoid uncertainty in the decision process. By anticipating future resource developments and rectifying deficiencies in functional resource data prior to the actual decision processes, decision makers can ensure that an allocation decision will be made under conditions of risk or certainty. With uncertainty no longer present in the decision situation, an allocative decision can be made which maximizes the benefits of development while maintaining the biophysical foundations of existing and future resource uses.

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Functional Redundancy of Stream Detritivores: an Experimental Test

by

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B.Sc., Queen's University, 1992

A Thesis Submitted in Partial Fulfillment of the
Requirements for the Degree of

MASTER OF SCIENCE

in the Department of Biology

We accept this thesis as conforming
to the required standard

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ABSTRACT

Relationships between species richness and ecosystem function may depend on the degree of functional differentiation vs. redundancy among coexisting species. Functional redundancy occurs when ecosystem function is maintained at nearly constant levels despite shifts in the populations driving that process. Detritivorous aquatic insect communities were experimentally manipulated by separately removing each of two dominant limnephilid caddisfly species to determine: (1) if species were functionally redundant, (2) if coexisting species interacted via inhibition or facilitation, and (3) if there were differential effects of intra- vs. interspecific density compensation. Per capita and per unit biomass effects of two response variables, leaf consumption (resource capture) and secondary production (insect growth) were compared. Density compensation was generally effective at maintaining leaf consumption after species loss, suggesting functional redundancy of the two caddisfly species. The two species, however, were not redundant for secondary production. *Psychoglypha prita* had significantly higher secondary production (during the experiment) than *Psychoglypha* sp. A. Treatments containing the two species in combination showed less leaf consumption and secondary production than predicted by 'null models' of no interaction, indicating inhibition (interspecific competition) between the two species. In monoculture, interference competition may have decreased individual growth. In summary, classifying these two species as redundant depends on the response variable considered.

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Introduction

Theoretical interest in the relationship between species diversity and the magnitude and stability of ecosystem processes has existed for decades (MacArthur 1955, Paine 1969, May 1972, Jones and Lawton 1995, Loreau 2000). Recently, accelerating extinction rates have stimulated empirical research on the relationships between species richness (number of species), species identity (community composition) and ecosystem processes (Schulze and Mooney 1993, Naeem et al. 1994, Tilman and Downing 1994, Tilman 1996, Aarsen 1997, Naeem and Li 1997, McGrady-Steed et al. 1997, Mikola and Setälä 1998, Symstad et al. 1998, Cardinale et al. 2000, Jonsson and Malmqvist 2000, Petchey 2000, Duffy et al. 2001, Jonsson et al. 2001, Ruesink and Srivastava 2001, Cardinale et al. 2002a, Jonsson et al. 2002, and others). Several studies have shown that as the number of species increases, ecological processes (e.g. decomposition, productivity, nutrient cycling etc.) increase in magnitude or stability (Naeem et al. 1994, Naeem and Li 1997, McGrady-Steed et al. 1997, Naeem 1998, Jonsson and Malmqvist 2000, Cardinale et al. 2002a). However, the contribution of number of species per se versus the effects of particular species on ecosystem functioning remains largely unexplored (but see Aarsen 1997, Symstad et al. 1998, Jonsson and Malmqvist 2000, Jonsson et al. 2002).

General models that predict an average relationship between the number of species and the magnitude of a response variable include the “rivet”, “redundancy” and “idiosyncratic” hypotheses. The “rivet” hypothesis (Ehrlich and Walker 1998) maintains that all species contribute to ecosystem function in a small, but significant way, whereas the “redundancy” hypothesis (Walker 1992) suggests that certain species drive ecosystem functioning, while other so-called passenger species contribute less to function. The "idiosyncratic" hypothesis states that even if a change in function can be forecast, its size and direction may be impossible to predict, i.e., there is no consistent effect of species richness or identity on ecosystem processes (Lawton 1994). Untangling the mechanisms that drive the general relationships between species diversity and ecosystem function requires an understanding of how the characteristics of coexisting species influence ecosystem processes.

Mechanisms by which species diversity can influence ecosystem functioning include a 'selection effect', where a particular species is competitively dominant (Aarssen 1997), a 'complementarity effect' that occurs through either resource partitioning (Hooper and Vitousek 1997), phenological complementarity (Stevens and Carson 2001) or facilitative interactions between species (Soluk and Richardson 1997, Cardinale et al. 2002a), and a 'stability effect' where multiple, functionally similar species within an assemblage provide 'biological insurance' against changes in ecosystem function after species loss (Naeem and Li 1997, Naeem 1998, Fukame et al. 2001). Compensatory responses by species are another mechanism by which nearly constant levels of ecosystem processes can be maintained after species loss (Frost et al. 1995). A 'functional' response could maintain levels of ecosystem function if there is an increase in the per capita effects of individuals, while a 'numerical' response could maintain levels of function if there is density compensation by other species (Ruesink and Srivastava 2001).

Density compensation was equated to functional redundancy by Walker (1992), who suggested that complete functional redundancy could only occur if, following the removal of one species, there was density compensation by the remaining species. This definition of redundancy was also used by Frost et al. (1995), who suggested that redundancy be defined as the maintenance of ecosystem function at nearly constant levels despite changes in the composition of species driving that process. Mechanisms for the redundancy hypothesis were proposed by Mikola and Setälä (1998) using the concept of niche. One possible mechanism involves modification of a species' realized niche when biotic interactions change. In this scenario, the remaining species use the newly released resources and replace the biomass and production of the lost species. This mechanism is similar to the functional response suggested by Ruesink and Srivastava (2001). A second proposed mechanism does not involve niche modification, but rather, some sort of interspecific release, e.g. competitive release upon the loss of one species. In this scenario, the coexistence of species is not facilitated by resource partitioning, thus, species occupy similar niches all of the time (Mikola and Setälä 1998). Through either proposed mechanism, unchanged biomass and productivity within functional groups results in unchanged ecosystem functioning (Walker 1992; Lawton and Brown 1993).

The degree of functional redundancy among co-occurring species is critical to testing the effects of species richness on ecosystem processes (Lawton 1994). The majority of recent studies that have demonstrated a relationship between species richness and ecosystem function have focused on primary producers in grassland communities or aquatic microbial communities (reviewed by Schläpfer and Schmid 1999). In contrast, consumer effects on resources have rarely been examined in this context. Studies that have explicitly tested functional redundancy among consumer species are rare (Harris 1995, Morin 1995, Kurzava and Morin 1998, Duffy et al. 2001, Mermillod-Blondin 2001). Moreover, even fewer studies have investigated the mechanisms that mediate interactions between consumer species, and their effects on ecosystem level processes (Jonsson and Malmqvist 2000, Duffy et al. 2001, Ruesink and Srivastava 2001, Cardinale et al. 2002a, Jonsson et al. 2002). There is evidence of competition within stream invertebrate grazer communities (Hart 1985, Hawkins and Furnish 1987, Lamberti et al. 1987, Kohler 1992, Cross and Benke 2002) and facilitation between collector species (Cardinale et al. 2002a). However, competitive or facilitative interactions between detritivore species (those feeding on detritus > 1 mm^2) are understudied (Jonsson and Malmqvist 2000, Ruesink and Srivastava 2001, Jonsson et al. 2002).

Headwater streams are an ideal model system with which to investigate relationships between species diversity and ecosystem function. Headwater reaches of stream ecosystems receive the majority of their energy as allochthonous leaf litter input, and decomposition of this leaf litter is an important ecosystem process (Wallace et al. 1999). Changes in the magnitude or stability of leaf decomposition can affect local detritivore communities as well as the productivity of downstream consumers that rely on the conversion of coarse organic matter to fine organic matter performed by leaf shredding detritivores (Short and Maslin 1977, Heard and Richardson 1995). Additionally, this input of organic matter often occurs as a seasonal pulse, for example, during autumnal leaf fall, with subsequent mobilization and redistribution during spring freshet events. Leaf detritus can therefore become seasonally limiting in streams (Richardson 1991, Dobson and Hildrew 1992), which can lead to intense competition or niche complementarity between detritivorous species. Aggregations of species in the same guild that exploit ephemeral resource patches such as stream leaf packs (Finn 2001) provide an ideal opportunity to test for functional redundancy and mechanisms maintaining species coexistence.

I tested several hypotheses in this study. First, I tested the "redundancy" hypothesis by quantifying the effects of two detritivore species in monoculture on two ecosystem processes, leaf consumption (resource capture) and secondary production (growth). Second, I tested for interactions between species by comparing species performance in monoculture to the performance of species in combination. Finally, I tested for density dependence of leaf consumption and growth, and for differential effects of intraspecific vs. interspecific density compensation.

Materials and methods

Study site

Experiments were conducted in 2000 and 2001 near Cranbrook, British Columbia, Canada (49°19′ N, 115°42′ W; Fig. 1). Richard Creek is a small, second-order tributary (1:20,000 map scale) of Gold Creek, and is located approximately 1550 m above sea level. The study reach was located 2.6 km downstream of the source of Richard Creek. Richard Creek drains a catchment underlain with sedimentary and metamorphic rock including quartzite, argillites, siltstones, sandstones and conglomerates (Deverney Engineering Services Ltd. 2002). Managed conifer forests dominated by lodgepole pine (*Pinus contorta*) and western larch (*Larix occidentalis*) with minor components of Engelmann spruce (*Picea engelmannii*), Douglas fir (*Pseudotsuga menziesii*), and subalpine fir (*Abies lasiocarpa*) cover almost all of the catchment area (C. Donaldson, Galloway Lumber Co., pers. comm.). The channel slope was ~4%, the width of the channel was 1-2 m (bankfull width), and the average water depth in riffles was ~ 5-10 cm at baseflow. The stream bottom

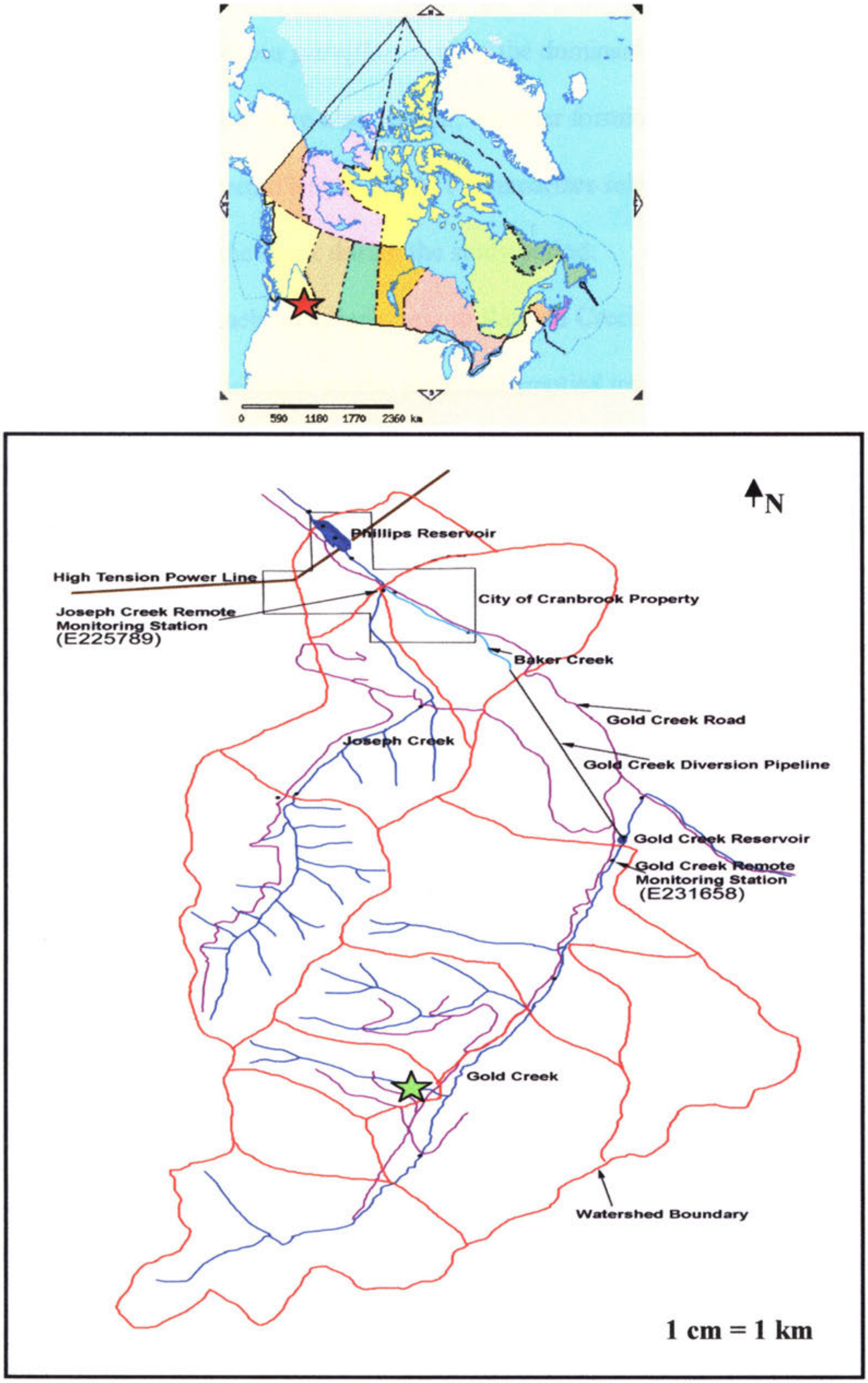

Figure 1. Location of study site near Cranbrook, British Columbia, Canada (denoted by star).

consisted primarily of cobble, gravel, and some moss-covered boulders. Sitka alder (*Alnus viridus*) and thimbleberry (*Rubus parviflorus*) were the dominant riparian species, but various other trees and shrubs were also present, together forming an almost closed canopy along most of the stream length. Table 1 summarizes selected physical and chemical characteristics of the creek during the study period.

Artificial stream channels were built next to Richard Creek (Fig. 2). Water flowed from the creek into two underwater intake pipes and emptied into 4 holding tanks (header boxes), which delivered water to 24 experimental channels in total (Figs. 3 and 4). Each experimental channel was 17.5 cm wide, 13.85 cm high and 1.2 m long. I added coarse gravel substrate (~ 4 cm diameter natural round gravel) to each channel, and placed 1 mm nylon mesh screens over the inflow, outflow and top surface to prevent organisms and detritus from colonizing or escaping the channels.

Insects and leaves

I chose two congeneric limnephilid caddisflies (Trichoptera) that are abundant in late summer in Richard Creek as my study organisms - *Psychoglypha* sp. A and *Psychoglypha prita* (Milne). Larvae of both species feed on detritus and are common inhabitants of western North American montane streams (Wiggins 1996). No adult specimens of *Psychoglypha* sp. A were caught during the study period, therefore, this species was unidentifiable beyond genus level. *Psychoglypha* larvae occur in a wide range of cool water habitats, ranging from springs to larger streams and their marginal pools. Larval cases are typically constructed of small rock fragments and pieces of wood combined into a straight tube up to 43 mm in length (Wiggins 1996). The two species were distinguished

Table 1. Physical and chemical characteristics of Richard Creek, Cranbrook B.C. between May and September, 2001. Physical characteristics measured by P. Jordan, B.C. Ministry of Forests (Nelson), water sample collected by L. Shama (01/05/18), and chemical characteristics measured by S. Leahy, MB Labs, Sidney, B.C.

Watershed area (ha)	~696
Discharge (m^3/s)	range: 0.5 to 1.0
Water temperature (°C)	range: 2.5 to 9.5
Alkalinity (mg/L)	94.2
NH_3-N (μg/L)	3.5
Colour (TCU)	7.9
Conductivity (μS/cm)	128
TKN (mg/L)	0.2
NO_3-N (μg/L)	27.9
NO_2-N (μg/L)	0.7
Ortho phosphorus (μg/L)	3.5
pH	7.6
Total phosphorus (μg/L)	10.0
Dissolved phosphorus (μg/L)	5.9
TDS (mg/L)	71.4
TSS (mg/L)	15.0
Turbidity (NTU)	0.9

Note: TCU = total colour units; conductivity (μS/cm) = micro Siemens per cm; TKN = total Kjeldahl nitrogen (organic nitrogen); ortho phosphorus = ortho-phosphate (bioavailable P); total phosphorus = all particulate and dissolved P; TDS = total dissolved solids; TSS = total suspended solids; NTU = nephelometric turbidity units.

Figure 2. Artificial stream channels (front view) built beside Richard Creek, Cranbrook, B.C., Canada (photo by L. Shama).

Figure 3. Intake pipes in Richard Creek that delivered water to artificial stream channels, Cranbrook, B.C., Canada (photo by L. Shama).

Figure 4. Artificial stream channels (side view), showing header boxes, outflow pipes, mesh screens, and 24 experimental channels (photo by L. Shama).

in the field based on differences in larval case construction. *Psychoglypha* sp. A constructs a triangular shaped case of smooth, round bark disks, whereas *Psychoglypha prita* constructs a round tube embellished with twigs, rocks and roughly shaped pieces of bark. Wiggins (1996) states that *Psychoglypha* larvae burrow into bottom gravel in the autumn as time for pupation approaches, however, the phenology of *P. prita* and *Psychoglypha* sp. A are unknown. At least one species of *Psychoglypha* (*P. subborealis*) is believed to overwinter in the egg stage (Wiggins 1996), but adults of other species have been collected alive on snow in winter and early spring (Denning 1970). Natural densities of *Psychoglypha* spp. in Richard Creek ranged from ~20 - 50 larvae per square meter during spring and summer months (Shama unpubl.). I quantified natural densities using Surber samples (0.3 m^2) taken ~monthly between May and October in both 2000 and 2001.

Non-target species of stonefly and mayfly larvae were also included in the experimental communities. I included one species of stonefly, *Yoroperla* sp., and two species of mayfly, *Baetis* sp. and *Paraleptophlebia* sp. These three species are common in Richard Creek as revealed by my Surber samples (Table 2). Stoneflies (Plecoptera) are primarily associated with clean, cool running waters. *Yoroperla* is a shredder-detritivore genus of stonefly that is distributed throughout the West in mountain and intermountain streams (Merritt and Cummins 1996). Mayflies (Ephemeroptera) occur in a wide variety of lentic and lotic habitats, the greatest diversity being found in rocky-bottomed, low-order, headwater streams. *Baetis* is a widespread genus of mayfly that comprises collector-gatherers of detritus and diatoms. *Paraleptophlebia* is another genus of mayfly that is also widely distributed, and contains species of collector-gatherers and facultative shredder-detritivores (Merritt and Cummins 1996).

Table 2. Common invertebrate taxa found in Surber samples collected from Richard Creek during spring and summer months in 2000 and 2001.

- Order Trichoptera
  - Family Limnephilidae
    - *Psychoglypha* sp. A
    - *Psychoglypha prita*
    - *Cryptochia* sp.
    - *Dicosmoecus atripes*
    - *Ecclisomyia* sp.
    - *Chyranda centralis*
  - Family Rhyacophilidae
    - *Rhyacophila verrula*
  - Family Glossosomatidae
    - *Glossosoma* sp.
- Order Plecoptera
  - Family Pteronarcyidae
    - *Pteronarcys* sp.
  - Family Peltoperlidae
    - *Yoroperla* sp.
  - Family Perlidae
  - Family Chloroperlidae
- Order Ephemeroptera
  - Family Baetidae
    - *Baetis* sp.
  - Family Leptophlebiidae
    - *Paraleptophlebia* sp.

I used Sitka alder leaves (*Alnus viridus*) as a source of food for experimental insect communities. Alder leaves are processed rapidly in streams compared to other detritus such as wood and conifer needles (Petersen and Cummins 1974). Alder leaves were collected from trees just prior to abscission in September 2000, and kept frozen until August 2001. I added 26.0 g (air dried for 24 h) of alder leaves to each of the 24 experimental channels. My choice of 26.0 g as the initial weight of alder leaves was based on estimated leaf consumption rates of *Psychoglypha* sp. A and *P. prita* determined in a preliminary feeding trial (see below). Leaf conditioning time at which detritivore shredding is maximal may take between 1-4 weeks. Leaf conditioning is the enhancement of leaf palatability for detritivores by microbial and fungal colonization (Gessner et al. 1999). Richardson (1992) found maximum invertebrate biomass on red alder leaves (*Alnus rubra*) 30 days after their introduction as unconditioned leaves. In this study, insects were introduced into experimental channels after leaves had been conditioned for one week.

Feeding trial

I conducted a one-day feeding trial on July 17, 2001 in ‘cages’ within artificial stream channels to estimate daily leaf consumption rates of *Psychoglypha* sp. A and *P. prita*. Cages were constructed of 6-9” lengths of 2” diameter PVC pipe with 1 mm nylon mesh fastened over both ends. The feeding trial consisted of 10 treatments. Nine treatments were each replicated 2 times: 100% *Psychoglypha* sp. A (at 3 initial stocking densities: 2, 4 or 8 caddislarvae); 100% *P. prita* (2, 4 or 8 caddislarvae); 50/50% *Psychoglypha* sp. A/*P. prita* (2, 4 or 8 caddislarvae); and a no-insect control treatment was replicated 6 times. For each experimental insect, I added 6 leaf disks (conditioned alder disks cut out with a 6 mm diameter hole punch). Replicates containing 2, 4 and 8 insects had 12, 24 and 48 leaf disks, respectively, at the start of the feeding trial. A subsample of leaf disks was dried for 72h at 50°C to estimate initial dry weight. At the end of the feeding trial, all insects were counted, dried (48 h at 50°C) and weighed, and all leaf material dried (72h at 50°C) and weighed.

In the 100% *Psychoglypha* sp. A treatment, individuals consumed 2.22 (± 0.30) mg of leaf per day (mean consumption ± SE of 6 replicates, averaged across all density treatments). In the 100% *Psychoglypha prita* treatment, individuals consumed 3.4 (± 0.30) mg of leaf per day (again averaged across all density treatments). Daily per capita leaf consumption rates differed between the two species because *P. prita* (mean biomass 3.22 ± 0.74 mg; n=27) was 9.9% larger than *Psychoglypha* sp. A (mean biomass 2.93 ± 0.16 mg; n=28). To account for differences in biomass among treatments and replicates, daily leaf consumption rates per unit biomass were calculated as: leaf consumption (initial - final leaf mass)/ [insect biomass (final dry weight)]*days. *Psychoglypha* sp. A consumed 0.82 (± 0.17) mg of leaf per mg of insect biomass per day (mean consumption ± SE of 6 replicates; all densities combined). *Psychoglypha prita* consumed 1.40 (± 0.16) mg/mg*day, and the two species in combination consumed 1.24 (± 0.10) mg/mg*day. Using the highest daily consumption rate (1.40 ± 0.16 mg/mg*day), I estimated how much leaf matter could potentially be consumed by 10, 20 or 40 caddislarvae over a period of 30 days. For example, if the average dry weight of an individual insect was 10 mg, 10 individuals would total 100 mg of insect biomass that could consume 1.40 mg of leaf per mg of insect/day * 30 days, equaling 4.2 g of leaf consumption (dry weight). Forty individuals (10 mg each) at the same daily consumption rate per unit biomass could consume 16.8 g of leaf matter over 30 days.

Experimental design

The experiment consisted of 10 treatments. Nine treatments were each replicated 2 times: 100% *Psychoglypha* sp. A (at 3 initial stocking densities: 10, 20 or 40 caddislarvae); 100% *P. prita* (10, 20 or 40 caddislarvae); 50/50% *Psychoglypha* sp. A/*P. prita* (10, 20 or 40 caddislarvae); and a no-insect control treatment was replicated 6 times (Table 3). Treatment densities were comparable to natural densities found in Richard Creek. The lowest density treatment (10 individuals) represented 'maximum potential per capita resource capture and growth', 20 individuals represented 'ambient density', and 40 individuals represented 'high density' of larvae. I measured case length of each caddislarvae individual prior to introduction, to estimate initial caddisfly biomass per experimental channel (using case length-biomass regressions, see below), and to estimate secondary production (i.e., growth) over the duration of the experiment.

Experimental communities were also established with a fixed number and sizes of non-target species of stoneflies and mayflies. Each experimental insect community contained 10 stoneflies (*Yoroperla* sp.) at ~1.12 mg each, and 20 mayflies (10 *Baetis* sp. and 10 *Paraleptophlebia* sp.) at ~1.0 mg each, resulting in approximately 31.2 mg (dry weight) of additional insect biomass. The experiment was conducted from August 1 through August 29, 2001, after which all insects were counted, dried (48 h at 50°C) and weighed, and all leaf material dried (for several days at 50°C) and weighed.

Table 3. Density treatments for *Psychoglypha* sp. A (A), *P. prita* (B), and the two species in combination (A/B).

	Experimental treatment									
	1	2	3	4	5	6	7	8	9	10
Psychoglypha sp. A	10A	20A	40A	5A	10A	20A	-	-	-	-
P. prita	-	-	-	5B	10B	20B	10B	20B	40B	-

Response variables

Net loss of leaf mass (g dry weight) was calculated as initial leaf mass - final leaf mass. Non-insect-caused leaf mass loss, i.e., microbial and fungal processing, leaching, and physical abrasion (Hieber and Gessner 2002), was estimated using the no-insect control treatment. Insect-caused leaf consumption (dry mg) was then calculated as: initial leaf mass (corrected for the mean net loss of leaf mass in the 6 no-insect control replicates) - final leaf mass.

I also measured shredder secondary production. As the approximate initial biomass of shredders in each replicate was known (via case length - biomass regression), and no known predators were present, shredder net secondary production can be estimated as the difference between initial and final biomasses (mg dry weight; Duffy et al. 2001). I estimated initial dry weight of experimental caddislarvae individuals from species-specific case length to dry weight regressions, based on caddislarvae collected from Richard Creek throughout the summer of 2001. Based on measurements of 39 larvae, initial weights of *Psychoglypha* sp. A individuals were estimated using the power function $Y=0.001(X)^{3.06}$, where X=case length (mm) and Y=initial dry weight (mg). Initial weights of *P. prita* individuals were estimated using $Y=0.002(X)^{2.91}$ (n=48). Additionally, I calculated the average daily growth rate of each species using: [*ln* (final weight/initial weight)]/days.

I calculated per capita and per unit biomass effects of the two response variables, leaf consumption and secondary production. Per capita effects were calculated as the change in consumption or production with increasing shredder abundance, i.e., the slope of leaf consumption (Y) vs. shredder abundance (X). Per unit biomass effects were calculated as the change in consumption or production with increasing shredder biomass, i.e., the slope of leaf consumption (Y) vs. shredder biomass (X). For experimental channels with missing caddislarvae, it was assumed that mortality occurred at the midpoint of the experiment. I also assumed that mortality followed a negative exponential function (Type III survivorship curve) over time. Hence, average shredder abundance over time was calculated as the geometric mean of initial and final abundance. Shredder biomass (average biomass at the midpoint of the experiment) was also calculated as the geometric mean of initial and final biomass.

Statistical analyses

Hypothesis 1: functional redundancy

I used one-way ANOVA to test for differences in net loss of leaf mass and secondary production among the experimental treatments. Significantly different treatments were identified using Tukey's post-hoc analyses. Within each insect treatment, there were three different initial densities, thus, by using one-way ANOVA, the within-treatment mean square (i.e., the residual variance) was inflated by differences in density. Hence, a more powerful model such as ANCOVA would incorporate differences in density and adjust for it, thereby increasing the probability of detecting differences among insect treatments.

I used ANCOVA models to test for differences in leaf consumption and secondary production (growth) among the three insect treatments using shredder abundance and shredder biomass as covariates. In the full ANCOVA model, I tested the homogeneity of slopes using the insect treatment*covariate interaction term. If the interaction term was not significant, i.e., the slopes were parallel, I tested the homogeneity of intercepts. Testing the homogeneity of intercepts tested for significant differences in elevation among insect treatments. Prior to statistical analysis, data were visually assessed for normality using quantile-quantile plots, and homogeneity of variances were assessed using Levene's test. All analyses were performed using SPSS (version 6.1.3). All means reported with ± 1 standard error unless otherwise stated, and I rejected the null hypothesis if the significance of p was ≤ 0.05.

Hypothesis 2: species interactions

I used three separate regressions to determine the per capita and per unit biomass effects of the two shredder species alone and in combination on the two response variables (leaf consumption and secondary production). Under the assumption of no non-additive effects (i.e., no inhibition or facilitation), I generated 'null models' for the expected impacts of the two species in combination. 'Null models' were calculated as the mean of the slopes and intercepts of the two species in monoculture. If there is inhibition, the impacts of the two species in combination should be less than that predicted by the 'null model' (suggesting that the interaction between the two species decreases overall consumption or secondary production). If there is facilitation, the impacts of the two species in combination should exceed that of the 'null model'. I tested for significant species interactions by comparing the mean slope of the two species in monoculture (i.e., the slope of the 'null model') to the slope of the two species in combination using Student's *t*-tests.

Hypothesis 3a: density dependence

I used separate ANCOVA models to test for density dependence of per capita leaf consumption and secondary production (per capita growth), and leaf consumption and growth per unit biomass. I predict that at higher densities, per capita and per unit biomass leaf consumption and growth would be less than that at lower densities due to resource limitation.

Hypothesis 3b: intra- and interspecific density compensation

I tested for differential effects of intra- and interspecific density compensation on per capita and per unit biomass resource capture and growth by comparing the slope of the 'null model' to the slope of the two species in combination using Student's *t*-tests. The slope of the 'null model' represented intraspecific density compensation, and the slope of the two species in combination represented interspecific density compensation. As above, I used three separate regressions to determine the per capita and per unit biomass effects of the three insect treatments on the two response variables (leaf consumption and secondary production) as a function of density. 'Null models' were then calculated as the mean of the two monocultures.

Results

Survivorship

Survivorship among caddislarvae was high for the experiment. Mean survivorship of caddislarvae for 16 of the 18 replicates that contained insects was 94.7 (± 2.89)%. There was low survivorship in two of the 100% *Psychoglypha* sp. A replicates (12.5% and 45.0%). These two replicates were excluded from the analyses of secondary production, as they had negative values for growth. Leaf consumption in these two replicates, however, was within the range of values for other replicates in that treatment, and were therefore included in the analyses of leaf consumption.

For each replicate, I calculated average shredder abundance using a linear and an exponential mortality model (Type II and Type III survivorship curves, respectively). For the linear mortality model, I calculated average shredder abundance as the arithmetic mean of initial and final abundance. For the exponential mortality model, I calculated average shredder abundance as the geometric mean of initial and final abundance. In each model, average shredder abundance occurs at the midpoint of the experiment (day 14). Average shredder abundance differed only slightly between the two mortality models, thus my use of the geometric mean of shredder abundance in the analyses was valid.

Survivorship was low among non-target stoneflies and mayflies for the experiment. Mean survivorship of stoneflies and mayflies for the 18 replicates that contained insects was ~13%, therefore, non-target insect biomass was excluded from all analyses. Possible sources of mortality for stoneflies and mayflies included starvation via interference from caddislarvae, stress resulting from non-optimal flow regimes, i.e., stream channel flow was faster than encountered in natural stream pools, and loss of individuals through adult emergence.

Leaf consumption

Net loss of leaf mass was 19.1% higher in insect treatments than in the no-insect control. One-way ANOVA showed that leaf mass loss was significantly higher in insect treatments than in the no-insect control ($F_{3,20}=6.28$; $p=0.004$; Fig. 5). There was, however, no significant difference in insect-caused leaf consumption among the three insect treatments. Although mean leaf consumption (i.e., for 23.33 insects over 28 days) of the 100% *P. prita* treatment was 81.1% higher than mean leaf consumption of the 100% *Psychoglypha* sp. A treatment, an ANOVA showed no significant difference among the three insect treatments ($F_{2,15}=1.38$; $p=0.281$; Table 4 and Fig. 5). Mean leaf consumption of the 100% *P. prita* treatment was 2050.41 (± 447.99) mg, 1132.09 (± 372.57) mg for the 100% *Psychoglypha* sp. A treatment, and 1714.78 (± 359.21) mg for the 50/50% *Psychoglypha* sp. A/*P. prita* treatment.

Per capita leaf consumption

Psychoglypha sp. A had higher per capita leaf consumption than *P. prita*, i.e., the slope of the leaf consumption vs. shredder abundance regression was steeper for *P.* sp. A than *P.prita*, but the difference in slopes was not significant. In the full ANCOVA model, the interaction of insect treatment and shredder abundance was not statistically significant. After removing the treatment*shredder abundance interaction term, the main effect of shredder abundance was statistically significant ($F_{1,14}=88.76$; $p < 0.001$) but treatment was not ($F_{2,14}=1.88$; $p=0.190$; Fig. 6 and Table 5). More insects ate more leaves, but there was no apparent effect of species composition on per capita leaf consumption.

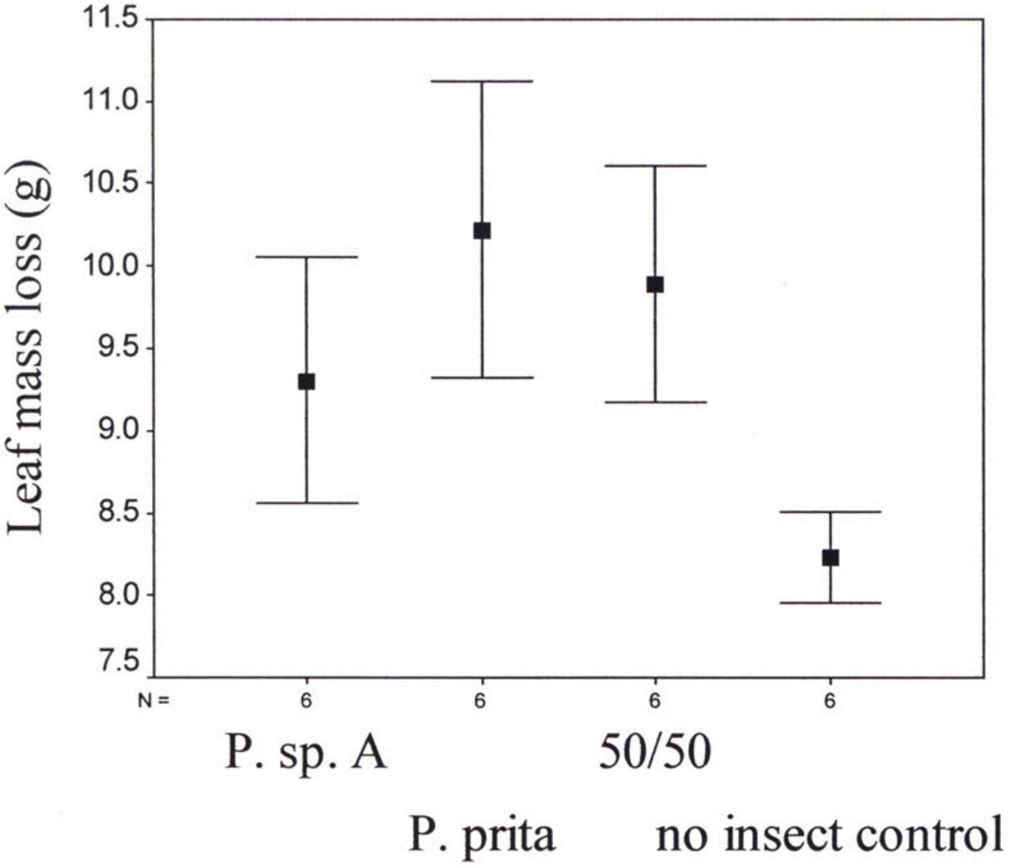

Figure 5. Mean (± SE, n=6) loss of leaf mass (dry g) over 28 days for the four experimental treatments (all densities combined).

Table 4. Analysis of variance of leaf consumption among the three insect experimental treatments (all densities combined).

Source of Variation	SS	DF	MS	F	p
Treatment	2590950.20	2	1295475.1	1.38	0.281
Error	14056158.66	15	937077.24		

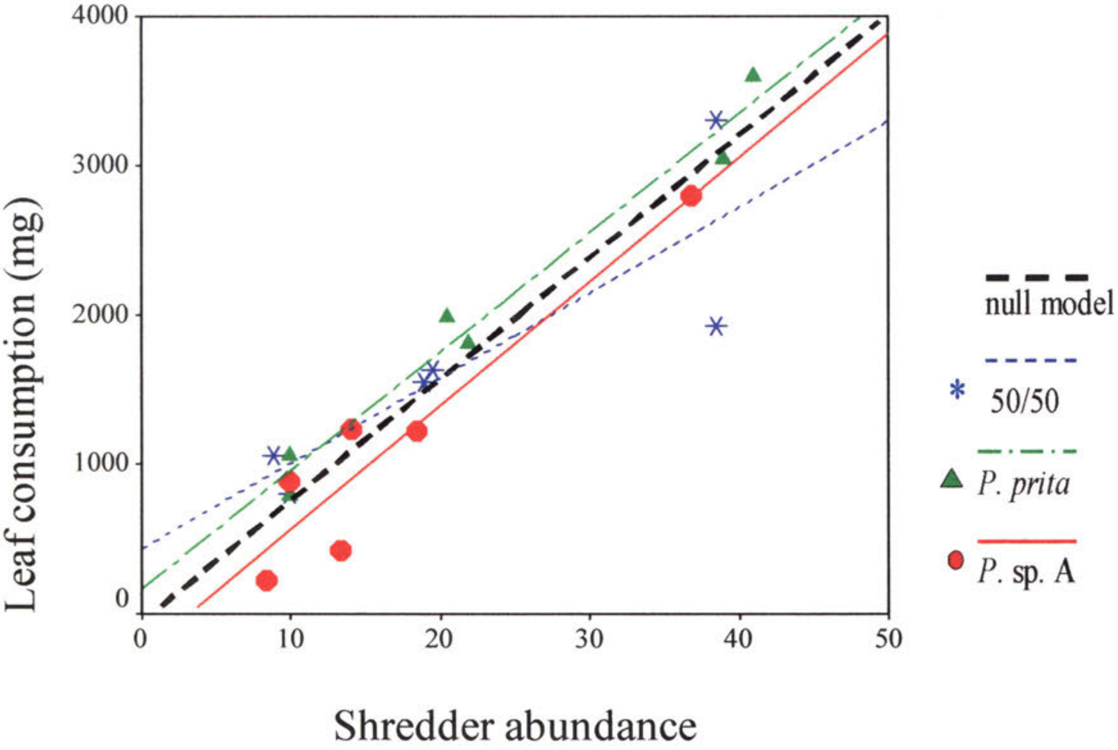

Figure 6. Per capita impacts on leaf consumption (dry mg) by shredder species alone, in combination, and in relation to a null model that predicts no facilitation or inhibition between species.

Table 5. Analysis of covariance of differences in leaf consumption among the three insect treatments using shredder abundance as a covariate.

Source of Variation	SS	DF	MS	F	p
Shredder abundance	12141230.04	1	12141230	88.76	<0.001
Treatment	513140.13	2	256570.07	1.88	0.190
Error	1914928.62	14	136780.62		

As expected, shredder abundance accounted for a large portion of the total variation in leaf consumption in each insect treatment. In the *P. prita*, *Psychoglypha* sp. A, and 50/50 treatment, abundance accounted for 97.2%, 89.7%, and 74.0% of the variation in leaf consumption, respectively (Fig. 6).

Leaf consumption per unit biomass

Psychoglypha sp. A had higher leaf consumption per unit biomass than *P. prita*, but the difference between the two species was not significant. In the full ANCOVA model, the interaction of treatment and shredder biomass was not statistically significant. After removing the treatment*shredder biomass interaction term, the main effect of shredder biomass was significant ($F_{1,14}=78.22$; $p< 0.001$) but treatment was not ($F_{2,14}=0.33$; $p=0.723$; Fig. 7 and Table 6). This shows that a higher insect biomass consumed more leaves, but again, there was no apparent effect of species composition on leaf consumption per unit biomass.

For each insect treatment, shredder biomass accounted for a large portion of the total variation in leaf consumption. In the *P. prita*, *Psychoglypha* sp. A, and 50/50 treatment, shredder biomass accounted for 87.7%, 87.2%, and 86.3% of the variation in leaf consumption, respectively (Fig. 7).

'null models': leaf consumption

I tested for interactions between the two species by comparing the observed species performance in combination (the 50/50 treatment) to 'null models' of the expected

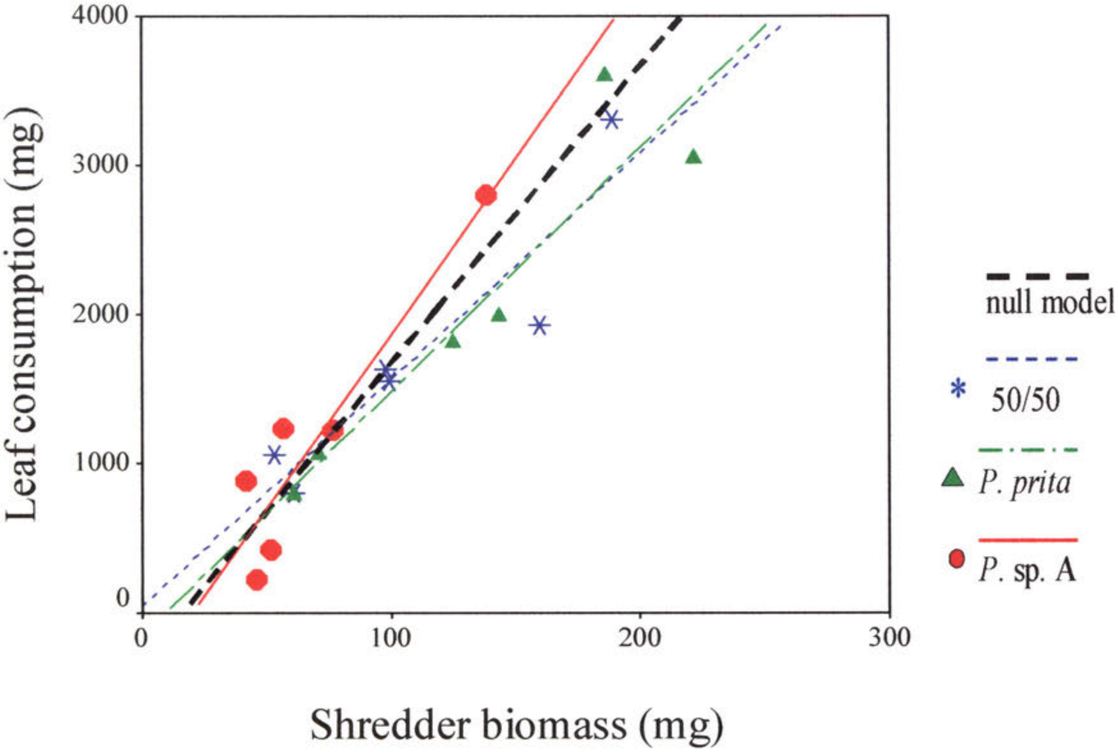

Figure 7. Per unit biomass (dry mg) impacts on leaf consumption (dry mg) of shredder species alone, in combination, and in relation to a null model.

Table 6. Analysis of covariance of differences in leaf consumption among the three insect treatments using shredder biomass as a covariate.

Source of Variation	SS	DF	MS	F	p
Shredder biomass	11922223.08	1	11922223	78.22	<0.001
Treatment	101326.48	2	50663.24	0.33	0.723
Error	2133935.58	14	152423.97		

performance of species in combination when there were no non-additive effects, i.e., no inhibition or facilitation. The interaction term in the full ANCOVA model used in previous analyses does not address non-additive effects, as the interaction term tests for differences among the three treatment slopes, not for differences between the 'null model' and the 50/50 treatment.

As indicated by the slopes, per capita impacts of the two species in combination (slope= 57.32 ± 17.0) was less than that predicted by the 'null model' (slope= 81.37 ± 7.75; Table 7 and Fig. 6). This suggested inhibition (interspecific competition) of per capita leaf consumption between the two species, although the difference in slopes was not statistically significant (two-tailed *t*-test: t=1.41, df=4; p=0.231). Similarly, the slope of leaf consumption per unit biomass of the two species in combination (slope= 15.17 ± 3.02) was less than that predicted by the 'null model' (slope= 19.91 ± 2.06; Table 7 and Fig. 7). Again, however, this difference was not statistically significant (two-tailed *t*-test: t=1.57, df=4, p=0.192).

Secondary production (insect growth)

Psychoglypha prita grew 118.3% more than *Psychoglypha* sp. A. One-way ANOVA showed that net secondary production (final - initial insect biomass) was significantly different among the three insect treatments ($F_{2,13}$=4.23; p=0.039; Fig. 8 and Table 8), and Tukey's post-hoc analysis showed that *P. prita* was significantly different from *P.* sp. A. Mean net secondary production (i.e., for 23.33 insects over 28 days) of the 100% *P. prita* treatment was 141.5 (± 20.91) mg , 64.82 (± 15.81) mg for the 100% *Psychoglypha* sp. A treatment, and 95.35 (± 15.23) mg for the 50/50% *Psychoglypha* sp. A/*P. prita* treatment

Table 7. Separate regressions of abundance and biomass effects on leaf consumption by two shredder species alone, in combination, and in relation to a 'null model' of no interaction between species.

variable	slope	(SE)	intercept	(SE)	F	p
#A	83.05	14.06	-269.22	272.31	34.88	0.004
#B	79.68	6.79	159.52	181.9	137.53	0.0003
#A/B	57.32	17.0	431.35	432.4	11.36	0.028
'null model'	81.37	7.75	-55.0	181.11	121.91	<0.001
A mg	23.48	4.49	-481.57	342.81	27.31	0.0064
B mg	16.34	3.05	-152.96	447.77	28.6	0.0059
A/B mg	15.17	3.02	44.95	364.04	25.24	0.0074
'null model'	19.91	2.06	-317.0	240.97	65.70	<0.001

(#A = *Psychoglypha* sp. A abundance; #B = *P. prita* abundance; #A/B = 50/50 abundance; A mg = *Psychoglypha* sp. A biomass; B mg = *P. prita* biomass; A/B mg = 50/50 biomass; 'null model' = mean of the slopes and intercepts of the two species in monoculture)

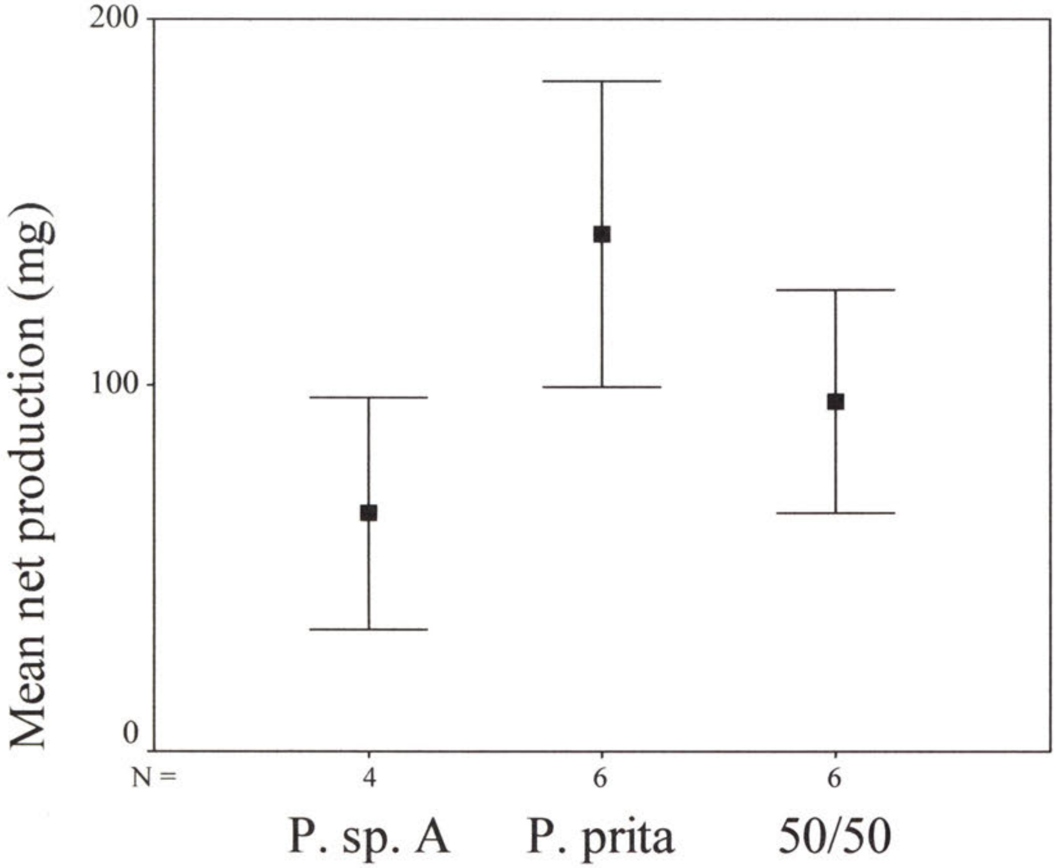

Figure 8. Mean secondary production (dry mg) over 28 days of the three insect treatments (all densities combined). Error bars indicate ± SE of the mean calculated from six replicate leaf bags (four replicates for 100% *Psychoglypha* sp. A treatment).

Table 8. Analysis of variance of secondary production among the three insect experimental treatments (all densities combined).

Source of Variation	SS	DF	MS	F	p
Treatment	15009.66	2	7504.83	4.23	0.039
Error	23076.35	13	1775.10		

Per capita growth

Psychoglypha prita had significantly higher per capita growth than *Psychoglypha* sp. A. Mean initial weights (based on case length-biomass regressions) of *P.* sp. A and *P. prita* individuals were 2.49 (± 0.07) mg and 3.52 (± 0.11) mg, respectively. Mean final weights of *P.* sp. A and *P. prita* individuals were 5.93 (± 0.33) mg and 8.54 (± 0.37) mg, respectively. Average daily growth rate (calculated using: [*ln* (final weight/initial weight)]/days) was higher for *P. prita* (0.037 mg/mg*day^{-1}) than *P.* sp. A (0.027 mg/mg*day^{-1}).

In the full ANCOVA model, the interaction of insect treatment and shredder abundance was not statistically significant. After removing the treatment*shredder abundance interaction term, the main effect of shredder abundance was statistically significant ($F_{1,14}$=12.95; p=0.004), as was treatment ($F_{2,14}$=5.88; p=0.017; Fig. 9 and Table 9). This result shows that although the slopes of the three insect treatments were homogeneous, i.e., no difference among slopes, there was a significant difference among intercepts. Therefore, there was an effect of species composition on per capita growth. Stated another way, although the slopes of the growth vs. abundance regressions were not significantly different between the two species, *P. prita* was larger than *P.* sp. A at the start of the experiment, and maintained this difference in size throughout the course of the experiment.

For each insect treatment, shredder abundance accounted for a large portion of the total variation in growth. In the *Psychoglypha* sp. A, *P. prita* , and 50/50 treatment, abundance accounted for 92.4%, 60.7%, and 30.3% of the variation in growth,

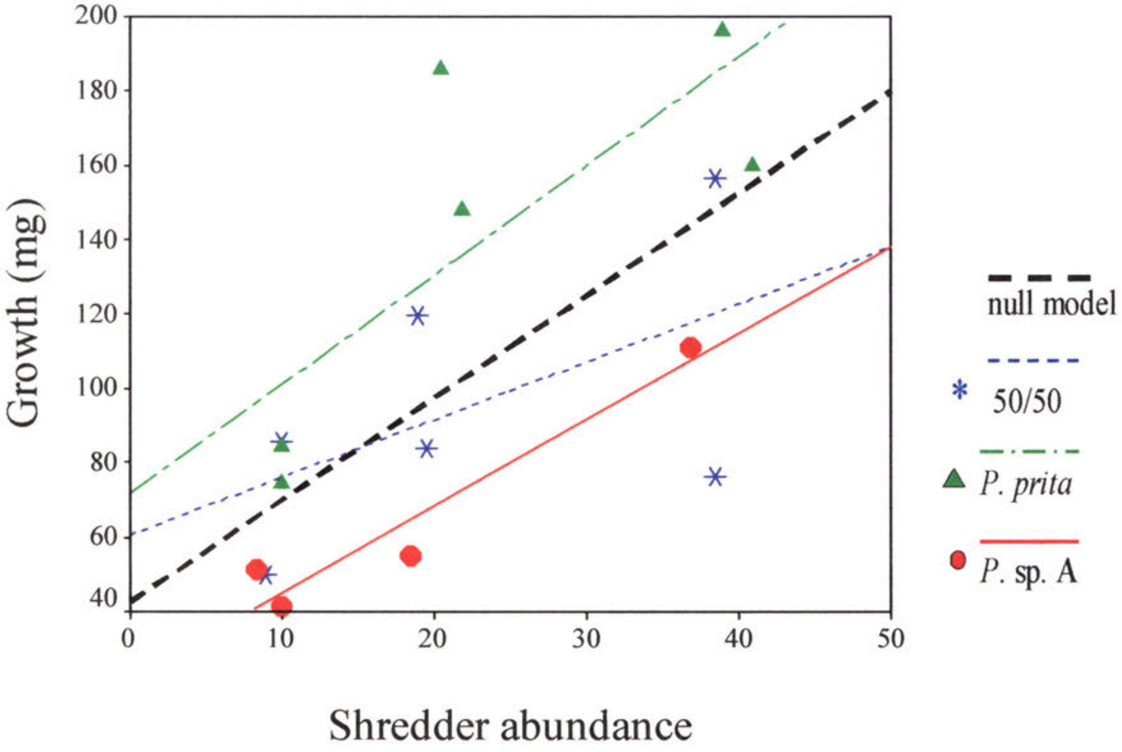

Figure 9. Per capita impacts on growth (dry mg) by shredder species alone, in combination, and in relation to a null model that predicts no facilitation or inhibition between species.

Table 9. Analysis of covariance of differences in secondary production (growth) among the three insect treatments using shredder abundance as a covariate.

Source of Variation	SS	DF	MS	F	p
Shredder abundance	11979.39	1	11979.39	12.95	0.004
Treatment	10876.50	2	5438.25	5.88	0.017
Error	11096.96	12	924.75		

respectively (Fig. 9).

Growth per unit biomass

Psychoglypha prita had higher growth per unit biomass than *Psychoglypha* sp. A, but the difference between the two species was not significant. In the full model, the interaction of insect treatment and shredder biomass was not statistically significant. After removing the treatment*shredder biomass interaction term, the main effect of shredder biomass was statistically significant ($F_{1,14}$=27.98; p<0.001), but treatment was not ($F_{2,14}$=3.36; p=0.070; Fig. 10 and Table 10). This result suggests that there was no apparent effect of species composition on growth per unit biomass.

For each insect treatment, shredder biomass accounted for a large portion of the total variation in growth. In the *Psychoglypha* sp. A, *P. prita* , and 50/50 treatment, shredder biomass accounted for 94.1%, 82.0%, and 45.9% of the variation in growth, respectively (Fig. 10).

'null models': growth

I tested for interactions between the two species by comparing the observed species growth in combination (the 50/50 treatment) to 'null models' of the expected growth of species in combination when there were no non-additive effects. As indicated by the slopes, per capita growth of the two species in combination (slope= 1.56 ± 1.18) was less than that predicted by the 'null model' (slope= 2.64 ± 1.09; Table 11 and Fig. 9). This suggested inhibition (interspecific competition) of per capita growth between the two

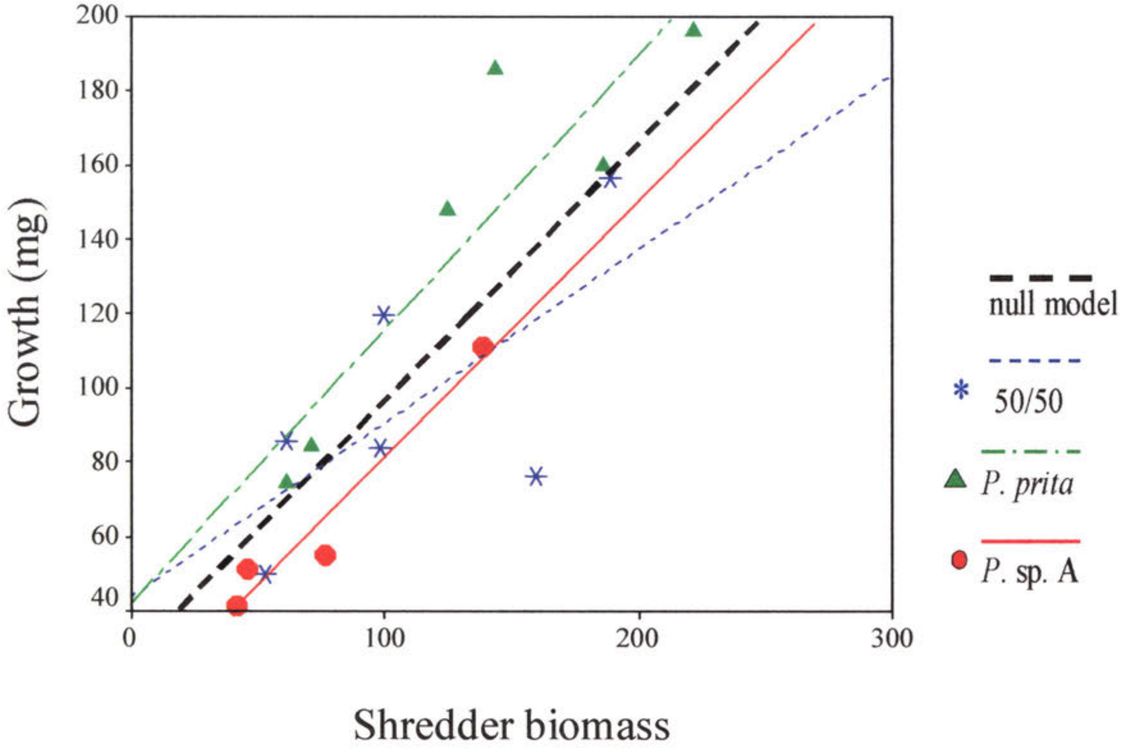

Figure 10. Per unit biomass (dry mg) impacts on growth (dry mg) of shredder species alone, in combination, and in relation to a null model.

Table 10. Analysis of covariance of differences in secondary production (growth) among the three insect treatments using shredder biomass as a covariate.

Source of Variation	SS	DF	MS	F	p
Shredder biomass	16149.89	1	16149.89	27.98	<0.001
Treatment	3875.38	2	1937.69	3.36	0.070
Error	6926.46	12	577.20		

Table 11. Separate regressions of per capita and per unit biomass effects on insect growth of two shredder species alone, in combination, and in relation to a 'null model' of no interaction between species.

variable	slope	(SE)	intercept	(SE)	F	p
#A	2.33	0.47	21.99	10.22	24.2	0.039
#B	2.94	1.18	71.79	31.68	6.17	0.068
#A/B	1.56	1.18	60.51	30.0	1.74	0.258
'null model'	2.64	1.09	46.89	27.19	8.80	0.018
A mg	0.69	0.12	12.59	10.35	32.09	0.030
B mg	0.74	0.17	42.06	25.28	18.28	0.013
A/B mg	0.47	0.25	43.75	30.72	3.39	0.140
'null model'	0.72	0.13	27.33	16.36	44.33	<0.001

(#A = *Psychoglypha* sp. A abundance; #B = *P. prita* abundance; #A/B = 50/50 abundance; A mg = *Psychoglypha* sp. A biomass; B mg = *P. prita* biomass; A/B mg = 50/50 abundance; 'null model' = mean of the slopes and intercepts of the two species in monoculture)

species, although the difference in slopes was not statistically significant (two-tailed t-test: t=0.915, df=4; p=0.412). Similarly, the slope of growth per unit biomass of the two species in combination (slope= 0.47 ± 0.25) was less than that predicted by the 'null model' (slope= 0.72 ± 0.13; Table 11 and Fig. 10). Again, however, this difference was not statistically significant (two-tailed t-test: t=1.00, df=4, p=0.374).

Density dependence

Per capita consumption vs. density

Psychoglypha prita had 40.9% higher mean per capita leaf consumption (averaged across all density treatments) than *Psychoglypha* sp. A, and per capita leaf consumption was not density dependent. Mean per capita leaf consumption (averaged across all density treatments) in the 100% *P. prita* treatment was 88.5 (± 4.59) mg of leaf, 62.8 (± 11.09) mg for the 100% *Psychoglypha* sp. A treatment, and 83.45 (± 8.92) mg for the 50/50% *Psychoglypha* sp. A/*P. prita* treatment (Fig. 11). In the full ANCOVA model, the interaction of insect treatment and density was not statistically significant. After removing the treatment*density interaction term, the main effect of density was not statistically significant (ANCOVA $F_{1,14}$=0.58; p=0.460) nor was insect treatment (ANCOVA $F_{2,14}$=2.69; p=0.103; Table 12). This suggests that species composition and differences in density had no apparent effect on per capita leaf consumption (resource capture). Stated another way, resources did not seem to be limited at high density.

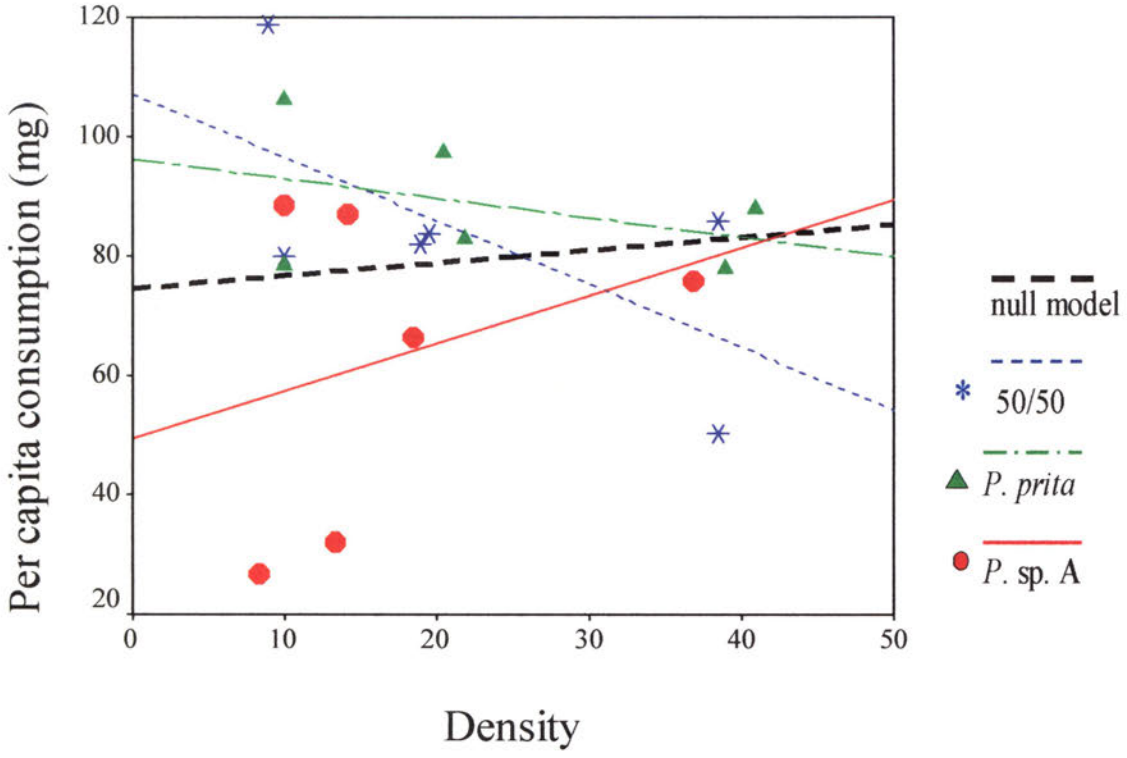

Figure 11. Per capita leaf consumption (mg) at increasing densities for the two shredder species alone, in combination, and in relation to a null model that predicts no interaction among species.

Table 12. Analysis of covariance of per capita impacts on leaf consumption of the three insect experimental treatments as a function of density.

Source of Variation	SS	DF	MS	F	p
Density	265.29	1	265.29	0.58	0.460
Treatment	2474.84	2	1237.42	2.69	0.103
Error	6443.78	14	460.27		

Leaf consumption per unit biomass vs. density

Psychoglypha sp. A had 3% higher mean leaf consumption per unit biomass (averaged across all density treatments) than *P. prita,* and leaf consumption per unit biomass was not density dependent. Mean leaf consumption per unit of insect biomass (averaged across all density treatments) in the 100% *Psychoglypha* sp. A treatment was 15.32 (± 2.92) mg of leaf consumed per mg of insect biomass, 14.87 (± 0.94) mg leaf/mg insect for the 100% *P. prita* treatment, and 15.82 (± 1.20) mg leaf/mg insect for the 50/50% *Psychoglypha* sp. A/*P. prita* treatment (Fig. 12). In the full model, the interaction of insect treatment and density was not significant. After removing the treatment*density interaction term, the main effect of density was not significant (ANCOVA $F_{1,14}$=0.69; p=0.420) nor was insect treatment (ANCOVA $F_{2,14}$=0.10; p=0.910; Table 13). Again, this suggests that species composition and differences in density had no apparent effect on resource capture per unit biomass.

Per capita growth vs. density

Psychoglypha prita had 66.3% higher mean per capita growth (averaged across all density treatments) than *Psychoglypha* sp. A., and per capita growth declined with density. Mean per capita growth (averaged across all density treatments) of the 100% *P. prita* treatment was 6.77 (± 0.81) mg, 4.07 (± 0.74) mg for the 100% *Psychoglypha* sp. A treatment, and 5.14 (± 0.92) mg for the 50/50% *Psychoglypha* sp. A/*P. prita* treatment (Fig. 13). In the full ANCOVA model, the interaction of insect treatment and density was not statistically

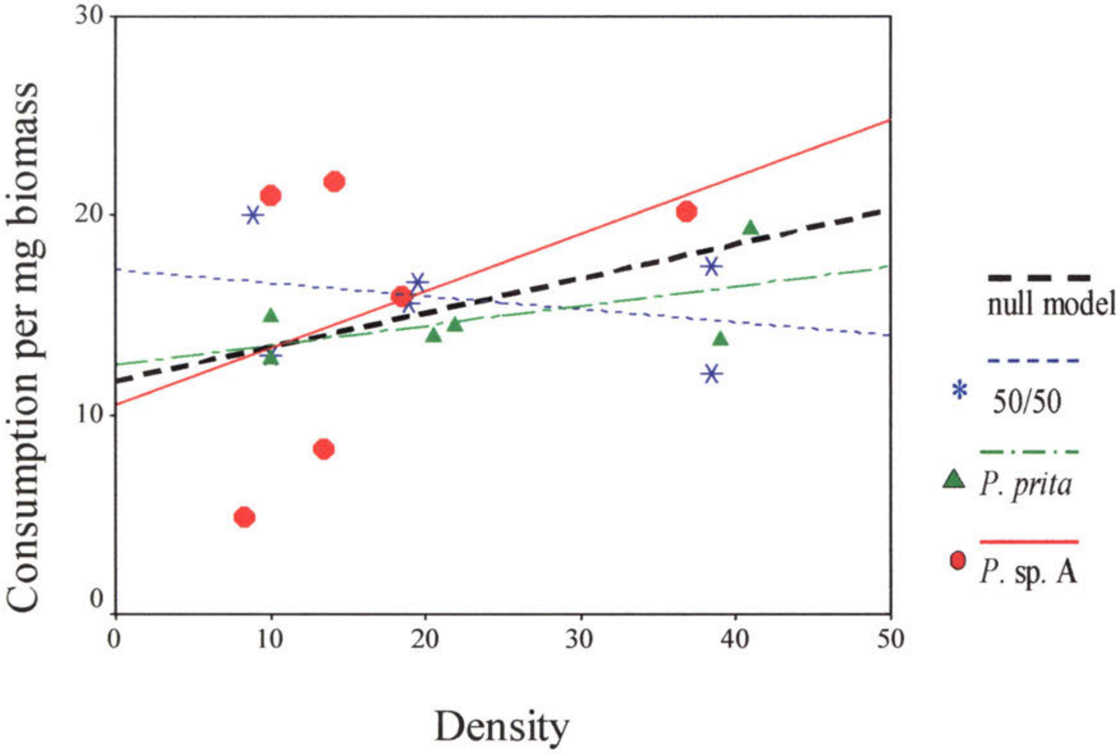

Figure 12. Leaf consumption per mg of insect biomass at increasing densities for the two shredder species alone, in combination, and in relation to a null model.

Table 13. Analysis of covariance of per unit biomass impacts on leaf consumption of the three insect experimental treatments as a function of density.

Source of Variation	SS	DF	MS	F	p
Density	15.29	1	15.29	0.69	0.420
Treatment	4.23	2	2.11	0.10	0.910
Error	310.39	14	22.17		

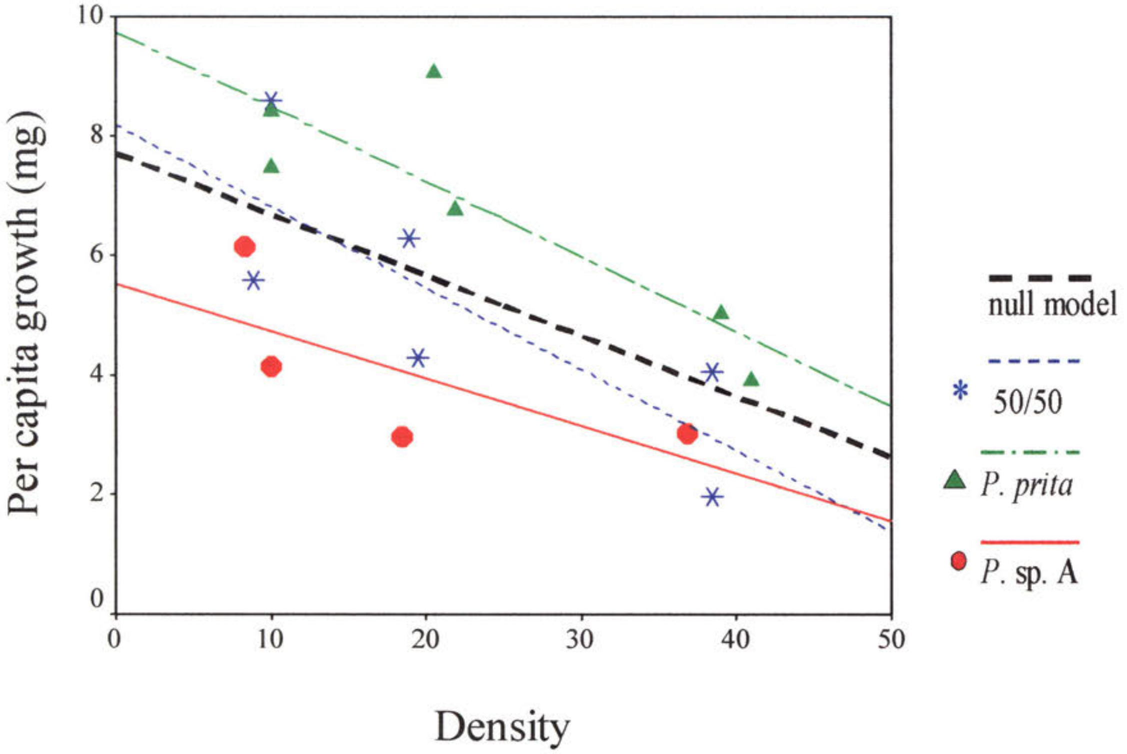

Figure 13. Density dependence of per capita growth (dry mg) of two shredder species alone, in combination, and in relation to a null model.

significant. After removing the treatment*density interaction term, the main effect of density was significant (ANCOVA $F_{1,12}$=20.83, p=0.001) as was insect treatment (ANCOVA $F_{2,12}$=8.52, p=0.005; Table 14). This suggests that species composition had a significant effect on per capita growth, and that growth decreased significantly at higher density.

Growth per unit biomass vs. density

Mean growth per unit biomass (mean weight gain per mg of insect, averaged across all density treatments) was 20.9% higher for *P. prita* than *Psychoglypha* sp. A, and growth per unit biomass declined with density. Mean growth per unit biomass (averaged across all density treatments) of the 100% *P. prita* treatment was 1.10 (± 0.07) mg, 0.91 (± 0.09) mg for the 100% *Psychoglypha* sp. A treatment, and 0.95 (± 0.13) mg for the 50/50% *Psychoglypha* sp. A/*P. prita* treatment (Fig. 14). In the full model, the interaction of insect treatment and density was not significant. After removing the treatment*density interaction term, the main effect of density was significant (ANCOVA $F_{1,12}$=14.21, p=0.003), but insect treatment was not (ANCOVA $F_{2,12}$=3.13, p=0.081; Table 15). This suggests that species composition had no apparent effect on growth per unit biomass, but that growth decreased significantly at high density.

Intra- and interspecific density compensation

I tested for differential effects of intra- and interspecific density compensation on per capita and per unit biomass leaf consumption and growth by comparing the slope of the

Table 14. Analysis of covariance of per capita impacts on insect growth as a function of density.

Source of Variation	SS	DF	MS	F	p
Density	32.70	1	32.70	20.83	0.001
Treatment	26.74	2	13.37	8.52	0.005
Error	18.84	12	1.57		

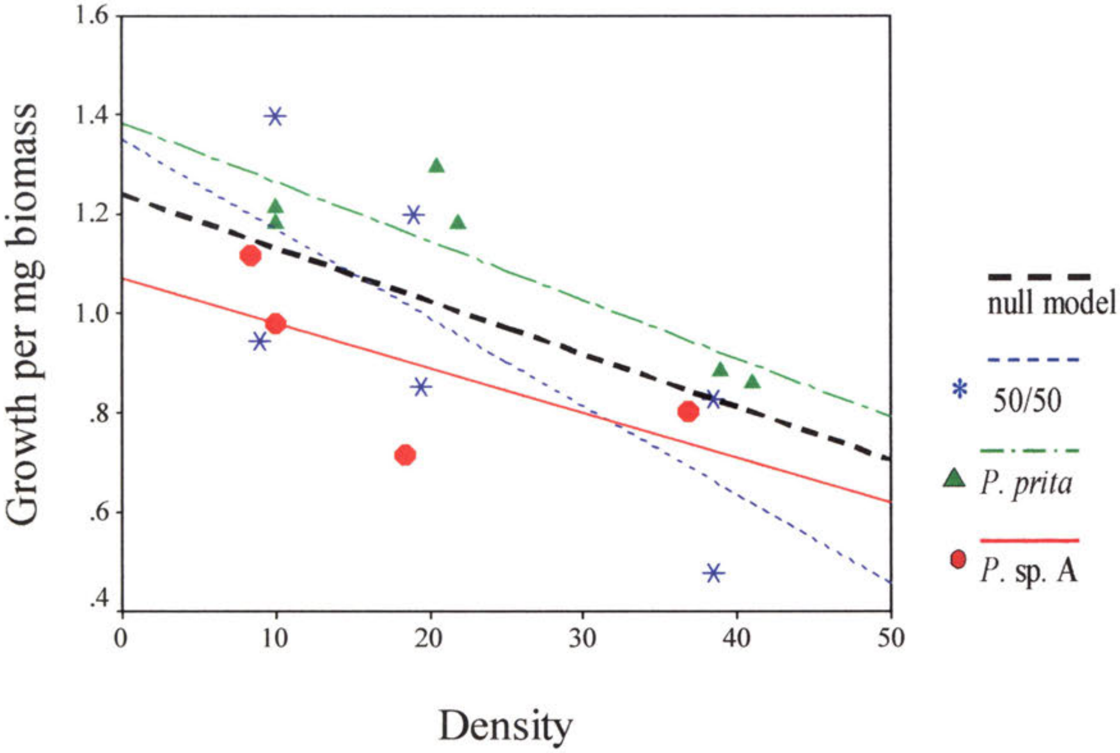

Figure 14. Density dependence of growth per unit biomass (dry mg) of two shredder species alone, in combination, and in relation to a null model.

Table 15. Analysis of covariance of per unit biomass impacts on insect growth as a function of density.

Source of Variation	SS	DF	MS	F	p
Density	0.42	1	0.42	14.21	0.003
Treatment	0.19	2	0.09	3.13	0.081
Error	0.36	12	0.03		

'null model' to the slope of the two species in combination. The slope of the 'null model' represents an average effect of intraspecific density compensation, and the slope of the two species in combination represents interspecific density compensation. In the previous ANCOVA models of density dependence, a significant main effect of density represents significant competition among individuals. However, to assess the relative strengths of intra- vs. interspecific competition, it was necessary to perform separate analyses between the 'null models' and the 50/50 treatments.

Leaf consumption

There were no differential effects of intra- and interspecific density compensation on per capita leaf consumption and leaf consumption per unit biomass. The slope of the 50/50 treatment (interspecific density compensation; slope= -1.06 ± 0.64) did not differ significantly from the slope of the 'null model' (intraspecific density compensation; slope= 0.24 ± 0.61; Table 16) for per capita leaf consumption (two-tailed *t*-test: t=2.05, df=4; p=0.110). Similarly, the slope of the 50/50 treatment (slope= -0.06 ± 0.11) did not differ significantly from the slope of the 'null model' (slope= 0.19 ± 0.12; Table 16) for leaf consumption per unit biomass (two-tailed *t*-test: t=2.41, df=4; p=0.074). As shown in the previous ANCOVA models of density dependence of leaf consumption, the main effect of density was not significant (Tables 12 and 13), therefore, individuals did not compete for leaf consumption. As expected, there was no detectable difference between the relative strengths of intra- vs. interspecific competition for leaf consumption.

Table 16. Separate regressions of per capita and per unit biomass effects on leaf consumption as a function of density of two shredder species alone, in combination, and in relation to a 'null model' of no interaction between species.

variable	slope	(SE)	intercept	(SE)	F	p
#A	0.80	1.24	49.27	24.06	0.42	0.554
#B	-0.32	0.38	96.17	10.21	0.72	0.444
#A/B	-1.06	0.64	107.18	16.15	2.78	0.171
'null model'	0.24	0.61	72.72	14.32	0.46	0.514
A mg	0.29	0.31	10.50	6.05	0.83	0.413
B mg	0.10	0.07	12.52	1.85	2.04	0.227
A/B mg	-0.06	0.11	17.28	2.71	0.37	0.575
'null model'	0.19	0.12	11.51	2.91	1.40	0.264

(#A = *Psychoglypha* sp. A abundance; #B = *P. prita* abundance; #A/B = 50/50 abundance; A mg = *Psychoglypha* sp. A biomass; B mg = *P. prita* biomass; A/B mg = 50/50 abundance; 'null model' = mean of the slopes and intercepts of the two species in monoculture)

Secondary production (insect growth)

There were no differential effects of intra- and interspecific density compensation on per capita insect growth and growth per unit biomass. The slope of the 50/50 treatment (slope= -0.14 ± 0.05) did not differ significantly from the slope of the 'null model' (slope= -0.10 ± 0.05; Table 17) for per capita growth (two-tailed *t*-test: t=0.650, df=4; p=0.551). Similarly, the slope of the 50/50 treatment (slope= -0.02 ± 0.01) did not differ significantly from the slope of the 'null model' (slope= -0.01 ± 0.005; Table 17) for growth per unit biomass (two-tailed *t*-test: t=0.938, df=4; p=0.401). As shown in the previous ANCOVA models of density dependence of growth, the main effect of density was significant (Tables 14 and 15), therefore, individuals competed for growth. Indeed, *P. prita* experienced significant intraspecific competition, and the two species in combination experienced strong interspecific competition for growth (Table 17). However, there was no detectable difference between the relative strengths of intra- vs. interspecific competition for growth.

Discussion

Functional redundancy of stream detritivores

Communities may contain species that perform very similar ecological roles (Walker 1992, Lawton and Brown 1993). If species are functionally redundant, then ecosystem processes can be maintained at nearly constant levels despite changes in species composition (Frost et al. 1995). My experiment used the simplest and least ambiguous experimental design to test this hypothesis. Ecosystem responses of two species were measured in isolation and

Table 17. Separate regressions of per capita and per unit biomass effects on growth as a function of density of two shredder species alone, in combination, and in relation to a 'null model' of no interaction between species.

variable	slope	(SE)	intercept	(SE)	F	p
#A	-0.08	0.06	5.54	1.24	1.92	0.300
#B	-0.13	0.04	9.75	1.01	11.10	0.029
#A/B	-0.14	0.05	8.18	1.30	7.00	0.057
'null model'	-0.10	0.05	7.65	1.32	2.34	0.165
A mg	-0.01	0.01	1.07	0.16	1.52	0.343
B mg	-0.01	0.003	1.38	0.09	13.14	0.022
A/B mg	-0.02	0.01	1.35	0.21	4.82	0.093
'null model'	-0.01	0.005	1.23	0.11	3.67	0.092

(#A = *Psychoglypha* sp. A abundance; #B = *P. prita* abundance; #A/B = 50/50 abundance; A mg = *Psychoglypha* sp. A biomass; B mg = *P. prita* biomass; A/B mg = 50/50 abundance; 'null model' = mean of the slopes and intercepts of the two species in monoculture)

compared to the response of a mixture of those species (Inouye 2001). The two species were expected, a priori, to function similarly, as they were congeners that occurred simultaneously on the same resource (stream leaf packs). I found that the two detritivore species were functionally redundant for one ecosystem process, leaf consumption (resource capture), but not redundant for a second response variable, secondary production (growth). These results were consistent with Duffy et al. (2001), who found that three species of grazing amphipods were functionally redundant for impacts on epiphyte accumulation, but were functionally different in impacts on eelgrass biomass and on grazer secondary production. Thus, the demonstration of functional redundancy in my study and Duffy et al.'s (2001) study depends on the response variable considered. These findings are corroborated by many analogous tests of plant diversity effects (reviewed in Schläpfer and Schmid 1999), and studies of vertebrate predator redundancy (Morin 1995, Kurzava and Morin 1998).

Psychoglypha sp. A and *P. prita* had similar overall effects on leaf consumption. However, per capita and per unit biomass impacts of the two species differed. Although no differences were statistically significant, *P. prita* had higher per capita leaf consumption, and *Psychoglypha* sp. A had higher leaf consumption per unit biomass. These results may be explained by small differences in body size of the two species. Species of similar body size exert similar per capita effects (Peters 1983), which was consistent with my overall result of effects on leaf consumption. However, larger individuals are predicted to have higher per capita effects than smaller individuals. Estimated initial weights of experimental insects (based on case length-biomass regressions) and final weights were higher for *P. prita*, which resulted in higher per capita impacts. Additionally, larger individuals have lower per unit biomass food requirements than smaller individuals, i.e., a shrew has to eat its body weight in food each day, an elephant does not (Peters 1983). Although the differences in body size of *P*. sp. A and *P. prita* were relatively small, *P*. sp. A individuals may have required more food per unit biomass to maintain their smaller body size. Accordingly, leaf consumption per unit biomass was higher for *P*. sp. A than *P. prita*.

Several recent studies have found significant differences among species for per capita impacts on some ecosystem level process, and have used this as evidence for diversity effects on ecosystem functioning (Jonsson and Malmqvist 2000, and others). However, in many cases, impacts per unit biomass were not measured (Cardinale et al. 2002a), or the authors included a short statement such as, "although, when biomass was used as a covariate in the analysis, there was no difference among treatments" (Jonsson and Malmqvist 2000). I maintain that species impacts per unit biomass should not be treated as caveats, as they more accurately reflect the metabolic capacity of the assemblage, and thus, their potential impacts on ecosystem processes (Ruesink and Srivastava 2001). This idea is supported by Morin (1995) who maintains that while per capita effects may change with species composition, effects standardized by biomass might be more robust to changes in species composition.

Psychoglypha sp. A and *P. prita* were not redundant for one response variable, secondary production. Secondary production refers to the formation of animal biomass over time, and is the product of growth rate and biomass (Huryn and Wallace 2000). Insect detritivores are responsible for a major fraction of total secondary production in many stream ecosystems, and they are critical links in the food web to higher trophic levels

(Wallace et al. 1999). Furthermore, secondary production may be the most important response to consider when investigating mechanisms of population or community regulation (Benke 1984). Since production has simultaneous effects on multiple trophic levels, the potential for strong biotic control of production clearly exists. However, few studies have addressed the effects of competition, predation etc. in controlling energy flows through food webs in stream ecosystems (Huryn and Wallace 2000).

In this experiment, *P. prita* produced more biomass on both a per capita and per unit biomass basis than *Psychoglypha* sp. A. Differences in production may be due to differences in growth rate and size of the two species. Average daily growth rate was higher for *P. prita* than *Psychoglypha* sp. A. Additionally, *P. prita* was larger than *Psychoglypha* sp. A throughout the experiment. More biomass and a higher growth rate resulted in higher production for *P. prita* over the course of the experiment. However, it is unlikely that a one month 'snapshot' of the two species' growth reflects what occurs throughout the year. Quantifying the intrinsic rate of growth for both species over the course of one full year (including winter months) could reveal temporal segregation of maximum growth between these two species.

Phenological complementarity (asynchrony of species' growth rates) has been found in several studies (Grafius and Anderson 1980, Duffy et al. 2001, Stevens and Carson 2001, but see Richardson 2001). Phenological complementarity may enhance ecosystem function when resources are ephemeral and different species peak at different times throughout the growing season (Stevens and Carson 2001). Such seasonal complementarity likely results in more constant levels of ecosystem processes on an annual basis due to an averaging of the effects of several independently varying species (Duffy et al. 2001). Among closely related taxa, however, phylogenetic constraint may result in overlapping phenology. In this case, temporal separation of resource use may not occur since major growth periods for congeners would overlap to some extent (Richardson 2001). However, Grafius and Anderson (1980) found an approximately three month separation of maximum growth rate between congeners of *Lepidostoma* (Trichoptera).

Kurzava and Morin (1998) state that any assessment of functional redundancy will depend on the measure used to assess the impacts of species on ecosystem processes. If this is a truism, how do we define functional redundancy? Walker (1992) maintains that complete redundancy only occurs when there is density compensation among remaining species. However, Lawton and Brown (1993) state that redundancy occurs when biomass or productivity levels are maintained despite changes in species composition. My results suggest that density compensation may not necessarily return biomass or productivity levels to antecedent conditions. Differences in body size, and thus, per capita impacts of species can result in different levels of ecosystem functioning. Similarly, return to antecedent total biomass may not maintain levels of ecosystem processes if that biomass is divided among more individuals of smaller body size. Many small individuals will not have the same metabolic capacity as fewer large individuals, as metabolic rate scales nonlinearly with body size (Peters 1983). Finally, many small individuals may compete for resources at high density, and thus inhibit one another and overall productivity (see below). These things considered together, in conjunction with my experimental results confirm the difficulty of defining functional redundancy.

Species interactions

The importance of species interactions in structuring stream communities has been demonstrated in a number of studies (Hawkins and Furnish 1987, Malmqvist 1993, Hill 1992, Kohler 1992, Kohler and Wiley 1997, Soluk and Richardson 1997, Cardinale et al. 2002a, Cross and Benke 2002, and others). The focus on abiotic factors in affecting the distribution and abundance of species has been re-evaluated in light of these recent studies. Harsh environmental conditions of streams, e.g. variable flow regimes, were thought to maintain population sizes at levels where resource limitation was unlikely and the impact of predators were negligible relative to abiotic factors (Hynes 1970). However, streams differ in the magnitude of discharge variation, and resource limitation and biotic interactions can be strong even during periods of relatively stable flow (Kohler 1992). In relatively stable habitats, interactions among individuals may increase as a result of the release of physical constraints on their distribution and growth (Cross and Benke 2002).

Leaf detritus represents a limiting resource that can result in intense competition or complementarity among stream detritivores (Richardson 1991, Dobson and Hildrew 1992, Finn 2001). In this experiment, I tested for species interactions using 'null models'. 'Null models' represented expected responses of the two species in combination if there were no non-additive interactions between them (Emmerson and Raffaelli 2000). If *Psychoglypha* sp. A and *P. prita* inhibited or facilitated one another, the response of the 50/50 treatments would deviate from the 'null model'. Although not statistically significant, both leaf consumption and secondary production (on a per capita and a per unit biomass basis) revealed inhibition (interspecific competition) between the two species. In all cases, the two species in combination performed worse than the 'null models'. Interspecific competition has been found in several studies that investigated taxonomically distant pairs of stream invertebrates (Hart 1985, Hawkins and Furnish 1987, Lamberti et al. 1987, Hill 1992, Kohler 1992, Kohler and Wiley 1997). For example, Kohler (1992) found significant interspecific competition between caddislarvae (*Glossosoma* sp.; Trichoptera) and mayfly larvae (*Baetis* sp.; Ephemeroptera). However, few experiments have tested congeneric species (Cross and Benke 2002). Congeneric pairs, through their similar resource requirements, are good study organisms for competition experiments because they are likely to compete.

Mechanisms of competition include exploitative (or consumptive) competition and interference competition. In exploitative competition, the interaction between individuals is mediated by a limiting food resource. Interference competition involves aggressive or non-aggressive encounters between individuals (Lamberti et al. 1987). In communities dominated by mobile taxa, at least two forms of non-aggressive encounters can occur. By contacting other individuals while moving, individuals can affect the ability of others to remain in habitats and the amount of time individuals are able to feed (Kohler 1992).

My results suggest that both exploitative and interference competition may have occurred between *Psychoglypha* sp. A and *P. prita*. Although not statistically significant, reduced per capita leaf consumption at high density for the two species in combination suggests that individuals ate less when neighboured with congeners, and deviation of the 50/50 treatments from the 'null models' was evidence of interspecific competition for food. Evidence for interference competition was revealed by analyses of density dependence. Per capita leaf consumption and consumption per unit biomass were not density dependent, whereas per capita growth and growth per unit biomass were density dependent. This suggests that at high density, individuals were capturing similar amounts of leaf matter as at lower densities, but were not converting it to biomass. In monoculture particularly, resources did not seem to be limited, yet individuals still experienced a decline in growth. Individuals may have experienced non-aggressive encounters with one another at high density, for example, and may have been 'knocked off' of food patches by mobile neighbours before food could be consumed. Several other studies have found evidence of both exploitative and interference competition (Lamberti et al. 1987, Hawkins and Furnish 1987, Kohler 1992), thus these two mechanisms may be common mediators of interactions between stream invertebrates.

Intra- and interspecific density compensation

By varying intra- and interspecific density compensation among treatments, the experimental design used in this study addressed two questions simultaneously for each species. First, did competition occur, and second, what were the relative strengths of intra- and interspecific competition for each species (Underwood 1986, Inouye 2001). Determining the relative strengths of intra- and interspecific competition allows for assessment of whether or not interspecific interactions affect the distribution and abundance of populations. If intraspecific competition is stronger, conspecifics may regulate populations to levels below those where interspecific interactions will be realized (Lawton and Hassell 1981, Underwood 1986, Lamberti et al. 1987, Cross and Benke 2002).

There were no differential effects of intra- and interspecific density compensation among *Psychoglypha* sp. A and *P. prita*. Neither intra- nor interspecific density compensation resulted in detectable competition for per capita leaf consumption and leaf consumption per unit biomass. However, I found significant intraspecific competition within *P. prita*, and strong interspecific competition between *P.* sp. A and *P. prita* for both per capita growth and growth per unit biomass. In all cases, however, the relative strengths of intra- and interspecific competition did not differ significantly from one another, which potentially allows these two strong competitors to coexist.

Competition experiments and issues of species coexistence are coupled with one another. Despite strong interspecific competition for the same limiting resource, *Psychoglypha* sp. A and *P. prita* continue to coexist. Competition theory predicts that stable coexistence should occur if the effects of intraspecific competition are stronger than the effects of interspecific competition for both species (Connell 1983). Although I found no statistical difference between intra- and interspecific competition, my results are consistent with this theory and the results of Cross and Benke (2002), in that coexistence among these two species may be mediated by slightly stronger competition among conspecifics than congeners.

Coexistence of competitors may also be mediated by spatial segregation (e.g. non-overlapping distributions), disturbance (e.g. changes in flow regime that can reduce population densities and 'reset' the system) and predation (Cross and Benke 2002). None of these three possibilities was investigated in this study, as experiments were conducted within mesocosms (artificial stream channels) that imposed spatial aggregation, experienced stable flow regimes throughout the study, and excluded predators within the experimental communities. It is unlikely, however, that spatial segregation mediates the coexistence of *Psychoglypha* sp. A and *P. prita*, as they co-occur on leaf packs in Richard

Creek. Disturbance is also an unlikely mediator of coexistence in this system, although rare flash floods may occur in Richard Creek, which can reduce population densities. However, I have shown that competition can be strong during periods of relatively stable flow conditions. Predation may prevent competitive exclusion through direct consumption of prey or indirectly by changing prey life history or feeding behaviour (Paine 1969, Peckarsky et al. 2002). Predation may mediate species coexistence in this system as trout and insect predators were both present in Richard Creek. However, this possibility remains untested.

Context dependency of functional redundancy

Species may appear functionally redundant under a restricted set of conditions, yet their functional roles may vary with environmental context (Cardinale et al. 2000, Duffy et al. 2001, Mulder et al. 2001, Wellnitz and Poff 2001, Cardinale et al. 2002b, Rosenfeld 2002). Environmentally mediated shifts in species function may be temporal or spatial. Phenological complementarity (as previously discussed) can result in relatively constant levels of ecosystem processes on an annual basis due to an averaging of the effects of several independently varying species (Duffy et al. 2001). Spatial environmental heterogeneity can also influence species' performances. The contributions made by individual species to overall ecosystem function can be shaped by differences in ecological performance across natural gradients. For example, a species may appear redundant at one point along an environmental gradient, but out-perform guild members at another (Wellnitz and Poff 2001).

Context dependency of functional redundancy has been illustrated theoretically and empirically. Wellnitz and Poff (2001) provide a theoretical example of how functional redundancy of stream grazers can depend on environmental context (low, medium and high current velocity). In their example, three species of stream grazers (A, B and C) are functionally equivalent in terms of their ability to remove attached algae from rocks at low current velocity. Similarly, if algal removal is averaged over all velocities, the three species have redundant mean effects. However, at medium velocity, species C outperforms other guild members, and at high current velocity, species B performs best. This example illustrates the importance of examining species function at multiple points along environmental gradients, yet few studies of functional redundancy have incorporated environmental heterogeneity (but see Mulder et al. 2001, Cardinale et al. 2002b).

Two recent studies provide empirical evidence of context dependency of species' function. Mulder et al. (2001) used species of mosses and liverworts to demonstrate that under constant conditions, species appeared functionally redundant, whereas under drought conditions, biomass increased with species richness through facilitative interactions among species. Cardinale et al. (2002b) demonstrated that primary productivity of stream algae and respiration of benthic biofilm increased in high-heterogeneity treatments more so than in low-heterogeneity treatments. The mechanisms responsible for the observed differences were physically mediated (alterations in near-bed velocity and turbulence intensity), and illustrate the influence of environmental context on species' function.

Detectable differences

Experiments of species' functional roles performed in homogeneous environments may bias results toward finding redundancy. In most experiments that examine species' functional roles and their interactions, environmental 'noise' is treated as a variable to control (Wellnitz and Poff 2001). In particular, mesocosm experiments (e.g. artificial stream channels) attempt to design as uniform an environment as possible. While uniform environments provide controlled, replicatable habitats in which to conduct experiments, they may not promote niche partitioning which would likely occur under natural conditions, and thus may bias results toward finding redundancy (Duffy et al 2001). Mesocosm experiments are still useful, however, as they can be used to test predictions at the scale of individual organisms, populations and communities, and permit quantification of mechanisms that mediate species interactions (Huston 1999).

Experiments that test for functional redundancy performed in uniform environments promote similarity of species' functional roles, and may fail to detect a difference between species when it actually exists if experimental power is low (Osler 2002). Power analysis allows for post hoc estimation of experimental power and the *a priori* estimation of sample sizes required to test hypotheses at set levels of power. Statistical power is defined as $(1-\beta)$, where β is the probability of failing to reject the null hypothesis (no difference among treatments) when it is false. Four things affect power: (1) choice of α level, (2) sample size, (3) effect size, and (4) residual variance (Underwood 1997).

Experiments can be constrained by many factors that limit the maximization of power. My experiment failed to detect a significant difference between *Psychoglypha* sp. A and *P. prita* for several response variables. In this particular case, the experiment was constrained by all four variables that affect power. Most importantly, however, power was constrained by low sample size, which was fixed at 24 artificial stream channels. For example, to detect a significant difference between the slope of the 50/50% *Psychoglypha* sp. A/*P. prita* treatment and the 'null' slope for per capita leaf consumption and leaf consumption per unit biomass, I would have needed to double the number of replicates from six (e.g. per capita consumption: two-tailed *t*-test: t=1.41, df=4; p=0.231) to twelve (two-tailed *t*-test: t=2.33, df=10; p=0.042). Similarly, to detect a significant difference between the 50/50 slope and the 'null' slope for per capita growth and growth per unit biomass, I would have needed to quadruple the number of replicates from six (e.g. per capita growth: two-tailed *t*-test: t=0.915, df=4; p=0.412) to twenty four (two-tailed *t*-test: t=2.20, df=22; p=0.039). These examples illustrate the need for power analyses in tests of species' roles in ecosystem function to determine variables such as minimum sample sizes necessary to detect differences among treatments. However, few studies in this area of research report any estimates related to experimental power (Osler 2002).

Conclusions

Classifying species as functionally redundant depends on the response variable considered. Species may have similar functional effects for one response variable, but not another. In this experiment, *Psychoglypha* sp. A and *P. prita* were functionally redundant for leaf consumption, but differed for another response variable, secondary production. Thus, in terms of assessing the functional redundancy of individual species, the fewer response variables measured, the more likely it is that species will be classified as functionally redundant (Rosenfeld 2002).

Psychoglypha sp. A and *P. prita* were competitors in this experiment. Interspecific competition reduced performance in species-combination treatments compared to the performance of monocultures. Walker (1992) and Lawton and Brown (1993) consider such competition strong evidence of functional redundancy among species. Interspecific release of resources (Mikola and Setälä 1998) and compensatory growth (Frost et al. 1995) were likely mechanisms by which levels of ecosystem processes could be maintained at nearly constant levels. Coexistence of these two strong competitors may be mediated by nearly identical relative strengths of intra- and interspecific competition.

Finally, intense interest in the ecosystem consequences of declining diversity has prompted numerous studies searching for general relationships between species diversity and process rates. At a mechanistic level, however, it is the characteristics of coexisting species that are fundamental to explaining the form of these general relationships. Future studies in this area of research need to investigate mechanisms that mediate species coexistence. Furthermore, studies should be conducted under environmentally heterogeneous conditions to simulate natural conditions. This experimental approach should increase the detectability of differences among species when they exist. This is not a trivial issue, as failing to detect differences among species when they exist is potentially dangerous from a conservation perspective.

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