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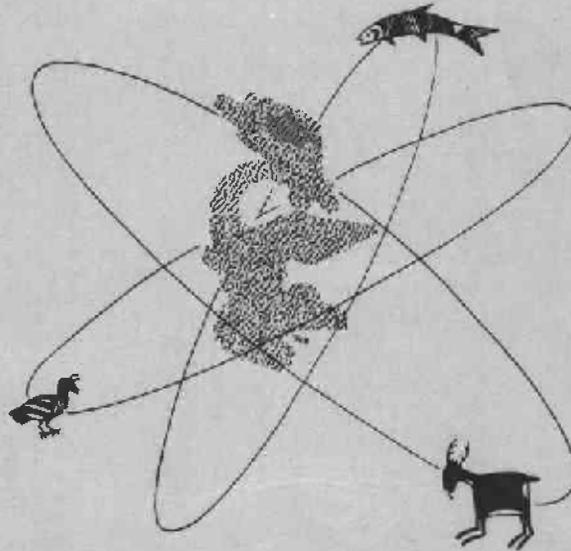
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AFS 62 STREAMFLOW REQUIREMENTS OF SALMONIDS

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## SUMMARY

This report attempts to summarize present understanding of the streamflow requirements of juvenile salmonid fishes, and to relate current methodologies used for recommending minimum summer streamflows for fish to those requirements. The objective of the review is to stimulate thought about ecological concepts important to the development of methods for determining minimum flows, rather than to recommend particular techniques.

Alteration in the flow regime of a stream initiates a complicated set of changes in environmental conditions that ultimately affects fish populations. The nature and degree of influence of these changes on different species of anadromous salmonids rearing in streams in summer are not well understood. Literature points to long-term and complex interrelationships between young fish and their environment (in which varied food, shelter, suitable space, and other needs are all of importance) as the probable reasons for a lack of understanding.

Shelter, an essential and complex element of fish habitat, can be influenced significantly by streamflow. In some streams the availability of vegetative borders which offer valuable shelter to fish may be closely related to flow. Densities of fish might be measurably increased by higher water velocities through increased use of substrate material as cover, and resultant visual isolation. A better understanding of what constitutes shelter is greatly needed, as is more study of the complex and varying cover needs of each salmonid species.

Aquatic and terrestrial invertebrates are of paramount importance as food for salmonids, and the manner in which streamflow affects these resources is of considerable significance. Substrate and water velocity are principal factors controlling the types and abundance of benthic invertebrates. A strong, positive correlation exists between velocity and the level of aquatic insect drift. The abundance of terrestrial insects entering streams is related to the proximity of shoreline vegetation, as is the amount of allochthonic energy supplied to the stream ecosystem. There appears, as well, to be considerable potential for either unnaturally fluctuating or unnaturally stable streamflows to adversely affect invertebrate fauna. Relationships between stream discharge and invertebrates need further study, particularly in such areas as the influence of flow on benthic production and drift abundance, and in long-term effects of more constant streamflow regimes.

Salmonid feeding activity, like food supply, is linked importantly with discharge level, particularly with water velocity. Much of the distribution of fish in stream channels is associated with feeding opportunity, yet much of it is also controlled by the physical environment. Salmonids are frequently territorial, and must depend on the availability of incoming food drift. Water current mostly determines the numbers of organisms transported to locations where fish reside. In reduced currents fish may resort to increased foraging and energy expenditure to obtain adequate food, which in turn could result in reduced growth. Since more space would be required to

obtain food, reduced carrying capacity would also be likely. In determining the effects of streamflow on salmonid feeding, consideration might also be given to possible relationships between diurnal and seasonal feeding patterns and schedules for release of water below dams.

Requirements of young salmonids for space, shelter, water velocity, or other habitat characteristics can be appraised in a more comprehensive and interactive manner through such concepts as territory or microhabitat. These concepts and some of the more obvious habitat interactions are discussed in this report. There are questions concerning such ideas that may be pertinent to a strict consideration of environmental requirements, such as whether territorial fish actually "require" water currents to maintain stability or whether, as many authors believe, current itself serves to induce territoriality. In a general way, it is fairly evident how conditions such as fluctuating discharge below hydroelectric installations might be highly disruptive to microhabitats or to territorial behavior of salmonids, thereby affecting productivity. It becomes increasingly difficult as the scope of such concepts broadens, though, to retain a quantitative character sufficient to allow application in actual field situations, either for estimating effects of potential habitat changes or determining specific conditions for maximum fish production.

Current methodologies for making minimum flow recommendations are limited by the level of understanding of stream ecology, though some approaches fail to take full advantage of known ecological prin-

principles. In developing methods for determining flows for salmonids under conditions of limited understanding, consideration should perhaps be given to achievement of an optimal balance between as many important needs of fish as possible. Improved understanding of the stream ecology of juvenile salmonids is seen as a more important immediate goal, however, than efforts to develop procedures for making streamflow recommendations.

## INTRODUCTION

### Background

Man's increasing demand for limited freshwater supplies is a threat to fish and wildlife resources that should be apparent even to the casual observer. Innumerable streams that once flowed briskly are now permanently dry, are periodically reduced to bare streambeds, or are partially dewatered during the summer or winter as the result of a great variety of water usage. The growing seriousness of the water supply problem with respect to aquatic life has been widely recognized among biologists, as indicated by Kelley, Cordone and Delisle (1960), and Fraser (1970, 1972). Historical, political and economical considerations and priorities, a burgeoning population, and lack of definitive biological information have severely hampered any recent efforts to reverse or even arrest the trend.

Oregon's early attempts to obtain biological data for use in determining adequate streamflows for protection of fish life began following enactment of revised water laws and establishment of a

Water Resources Board in 1955 (Pitney, 1969). The Oregon Wildlife Commission was subsequently given the responsibility of recommending to the Water Board adequate streamflows for all Oregon watersheds. Pitney (1969) reviewed the Wildlife Commission's early program, pointing out where advancements were made and problems arose. The factor which appeared to be most important in determining abundance of anadromous trout and salmon in Oregon was the number of juvenile fish surviving in streams through the summer low-flow period. He noted that it was difficult to make flow recommendations for that period or to support those made with factual data, because the requirements of juvenile fish were poorly understood. The increased summer demands for water for irrigation and other purposes heightened the importance of setting adequate flow levels for this period.

For some time the Environmental Management Section of the Oregon Wildlife Commission sought published information that would aid them in making recommendations of summer streamflow levels adequate for satisfactory production of fish. Experiencing limited success, a research project leading to development of improved methods for recommending flows was formally requested in 1968. A preliminary survey of information regarding summer streamflow requirements of juvenile anadromous salmonids was subsequently approved and was initiated on July 1, 1971.

#### Literature Search

A variety of library reference services, bibliographies and other sources were surveyed for significant literature pertain-

ing to the effects of streamflow on fish production. States and other agencies with ongoing investigations were also contacted and requests were made for unpublished, up-to-date information. A bibliography of particular usefulness was that prepared by Fraser (1970) on the establishment of acceptable flows for fish life. A revised and considerably more comprehensive bibliography has recently been published (Fraser, 1972). A review similar to that reported herein has also recently appeared (Hooper, 1973). A great number of current water research projects were found summarized in volumes of the Water Resources Research Catalog published by the Water Resources Scientific Information Center, Office of Water Resources Research, U.S. Department of the Interior. This latter source differed from most aquatic biology listings in that strictly hydrological studies were included.

Other than a limited number of obscure or subsequent references, little more specific, highly useful information pertaining to summer requirements of juvenile salmonids was discovered in the literature than had been located earlier by the Environmental Management staff of the Oregon Wildlife Commission. The great majority of papers dealing with flow requirements of fish either concerned spawning criteria, or flows needed to sustain sport fisheries for resident trout and other species in tailwaters below dams. These were often subjective and of limited value in providing information on the needs of juvenile anadromous fish in free-flowing streams. Other authors also noted the lack of information on rearing salmonids (Elser, 1972; Kraft, 1972; Tennant, 1972; Thompson, 1972; Hooper, 1973).

### Complexity of Stream Ecosystems

The most apparent reason for the general scarcity of literature relating to rearing requirements of fish or to methodology for recommending flows for this period is the obvious complexity of the stream ecosystem and the broad influence that stream discharge has on the environment of juvenile fish. Some comments by McFadden (1969) clearly indicate the task confronting those wishing to understand salmonid ecology or to develop criteria for assessing the impact of environmental changes. He notes that the early life stages (fry and parr) are influenced by extremely complex population processes, and that it is impossible to identify any one factor as a single or most limiting or regulating process. He states further that the operation of each factor can be understood properly only within the context of the network of relationships. Ruggles (1966) noted that there are so many variable factors in the natural environment, it is often difficult to collect enough data to permit the thorough statistical analysis that is needed for separating the effects of the factors. Additional problems were recognized by Cummins (1966) following his attempt to summarize and synthesize literature on stream ecology. He found the poor communication between ecologists concentrating on various aspects of stream systems to be most significant. A second major problem concerned the almost complete lack of uniformity of study methods.

The major, direct, cause and effect relationships that exist in the stream environment, emphasizing the influence of stream discharge,

have been modified from other publications and summarized in Figure 1. This diagram is neither all-inclusive, nor does it indicate in detail the intricate, often reciprocal pathways through which aquatic animals such as fish are affected by changes in streamflow. Most past approaches to the study of such complex systems have depended on control of the many variables through the use of artificial environments or other methods, painstaking procedures that frequently require many years before useful field applications are developed.

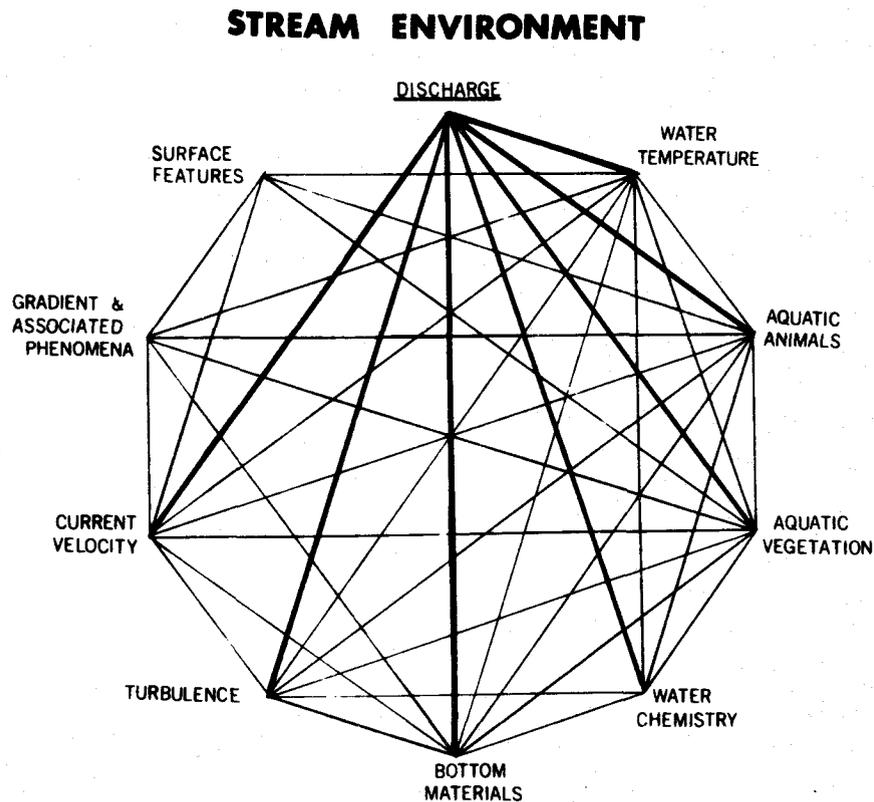


FIGURE 1. Major interactions between stream discharge and the aquatic environment. Arrows have not been included since many of the relationships are two-way.

In order to better understand some of the interrelationships that exist in the stream ecosystem, most recognizable factors can conveniently be separated into three principal components - hydrogeographic, chemical and biotic. The hydrogeographic component includes such channel geometry characteristics as gradient (slope), bed roughness and type, meander (sinuosity), cross-sectional relationships, etc., and includes hydraulic or flow characteristics such as area, pool:riffle composition, water velocity, depth and width. The chemical component might include aspects of water quality such as turbidity dissolved oxygen, and so forth. The biotic component encompasses broad categories such as primary production, ecology of stream invertebrates, aquatic and shoreline vegetation, and ecology of fishes. The vast majority of previous and current investigation of components of the stream system has unfortunately been rather specialized and has given little consideration to interactions. This report will be an attempt to review and associate some of the many factors influencing fish populations, but will not cover some of the more fundamental elements of the stream ecosystem such as initial energy sources and their early pathways. Neither will it cover in much detail water quality aspects, although under some circumstances of flow, such factors as water temperature might be of major significance in influencing aquatic biota.

#### Broad Review of Existing Literature

A substantial number of papers were located that made some reference to relationships between streamflow and aquatic life.

Many of these, however, spoke only in general terms, and many others were of little value in clarifying relationships or establishing water needs of aquatic life. Publications that contained significant information concerning water requirements or data on establishment of minimum flows for fish life included Delisle and Eliason (1961), Ruggles (1966), Hill and Burkhard (1967), Idaho Water Resources Board (1969), Collings, Smith and Higgins (1970), Pearson, Conover and Sams (1970), Chrostowski (1972), and the series of Basin Investigation reports from Oregon as exemplified by Thompson and Fortune (1970). These combined reference sources did not appear to warrant synthesis into broad guidelines for establishing flow recommendations, some being based on subjective determinations.

Published information relating fish populations to habitat factors other than streamflow was generally more available. Substantial numbers of papers were found in which cover (shelter), pool:riffle periodicity, and water depth were discussed. Less extensive coverage of factors such as water quality was evident.

Literature on growth, behavior, movement and production of salmonids was fairly extensive, while that on competition was limited. Less than half of the reports that concerned these factors mentioned water velocity or stream discharge, however, and the number of sources containing significant material on the interrelationships of these factors was again quite limited. Important papers linking fish production with streamflow in some manner were Smoker (1956), Ruggles (1966), Wipperman (1967, 1968, 1969), Kraft (1968, 1972), Corning (1969), Elser (1969), and Burns (1971).

A number of publications that considered relationships between streamflow and aquatic invertebrates were located, but again about half of these spoke only in general terms or were theoretical rather than technical in nature. It was apparent in the review of literature that many studies of fish populations in streams either gave too little consideration to invertebrates or omitted them completely from the design. Adequate study of invertebrate populations is difficult and time-consuming, a fact which may partly explain why more information has not been obtained by fishery workers. The more important sources of information on this subject were Briggs (1948), Surber (1951), Needham and Usinger (1956), Delisle and Eliason (1961) Ruggles (1966), Weber (1966), Kennedy (1967), McClay (1968), and Corning (1969). Among these, Kennedy perhaps supplies the most extensive and detailed information.

A number of general treatises concerning production, competition and behavior among salmonids in freshwater are valuable as summaries of past work and also as points of view in examining relationships between salmonid populations and the aquatic environment. Some of these provide general theories and useful approaches that may be applicable to the development of methodology for flow recommendations or to the design of new research. A partial list includes Larkin (1956), Newman (1956), Kalleberg (1958), Neave (1958), LeCren (1965), Chapman (1966a), Allen (1969), Chapman and Bjornn (1969), and McFadden (1969).

There are several anadromous salmonid species of importance in Oregon, including winter and summer steelhead, Salmo gairdneri,

cutthroat trout, S. clarki, coho salmon, Oncorhynchus kisutch, and spring and fall chinook salmon, O. tshawytscha. Obvious, subtle, and no doubt obscure differences exist among juveniles from these groups with respect to environmental requirements, largely because of the degree of variability in life history patterns and behavior. Data on streamflow requirements of each species are needed, and in this regard the available literature was of limited assistance.

Among the papers included in this bibliography that deal with all salmonids, roughly one-third are concerned with anadromous species in Oregon. The remainder are concentrated primarily on resident populations of rainbow trout or brown trout, S. trutta. The majority of reported data on environmental requirements of anadromous salmonids concerned coho salmon, followed in order by chinook salmon and steelhead trout. Material on cutthroat trout and summer steelhead was nonexistent.

Several publications not previously mentioned that were especially valuable in providing insight into the many factors and interrelationships inherent in stream ecosystems were Ambuhl (1959), Minckley (1963), and Hynes (1970).

#### Summer vs. Winter Population Control

Since this review proceeds from a basic premise that the summer-fall low streamflow period is of major importance in determining production of juvenile salmonids to the smolt stage, the question is certain to arise as to whether this season is more critical than,

say, the winter period. There seems to be some agreement that seeding of streams by anadromous species is usually adequate, with control of densities generally occurring at a later date (Chapman, 1966a; Pearson, Conover and Sams, 1970; Burns, 1971). Subsequent to emergence, the periods most likely limiting population size and growth would seem to be the low flow and winter seasons. Some are of the opinion that winter conditions in streams could impose greatest restrictions, but there appears at present to be little information from which to draw in support of this view.

A substantial number of authors have suggested or demonstrated relationships between stream discharge and juvenile or adult production for several species of salmonids in the Pacific Northwest, some correlations involving minimum summer flows (Wickett, 1949; McKernan, Johnson and Hodges, 1950; Henry, 1953; Neave and Wickett, 1953; Smoker, 1953, 1956; Neave, 1958; Pitney, 1969; Pearson, Conover and Sams, 1970; Burns, 1971). Many of these reports will be discussed in a later section of this review. As Chapman (1966a) indicated, "more water obviously provides habitat (space) for more fish", and it is primarily the logic of this relationship that has led many to believe that the low streamflow period is the most limiting. On the West coast, Burns (1971) provided detailed evidence supporting a positive flow-production relationship. He found in California streams that decreasing availability of living space caused the greatest mortality of young salmonids, with total mortality highest in the summer of lowest streamflow. Subsequent winter survivals, however, were not determined in Burns' study.

Chapman (1966a) suggests that in winter the availability of suitable space plays a dominant role in governing carrying capacity of streams. Certainly the importance of food relationships diminishes in winter, as do, in milder climates, some problems associated with water quality (temperatures, etc). Very low temperatures can apparently be detrimental to salmonids in some areas, however. McKernan, et al., (1950) found that low summer flows and exceptionally high winter floods seemed to result in poor subsequent runs of adult coho salmon along the Oregon coast. Their data suggested that in most years winter conditions were not so severe that summer population levels failed to carry through to some degree, and that suitable space may have been reduced by severe floods. Both summer and winter conditions are probably important, and the relative influence of either might be dependent in part of climatic differences between regions.

#### STREAMFLOW AND FISH SHELTER

Shelter, or cover, has long been recognized as one of the basic and essential elements of fish habitat. Shelter serves as a means of predator avoidance, and in streams may also provide areas of moderate current speed utilized as resting areas by fish. Any consideration of the ability of an aquatic habitat to support fish should take into account the influence of cover. Cover for fish in streams can be provided by overhanging vegetation, undercut banks, submerged vegetation, submerged objects (stumps, logs, roots, rocks), floating debris, and water turbu-

lence. It can be visualized that the amount or quality of shelter of different types could vary significantly with the level of discharge in streams.

The cover requirements of mixed populations of salmonids are not easily determined. Shelter needs may vary diurnally (Kalleberg, 1958; Allen, 1969; Chapman and Bjornn, 1969), seasonally (Hartman, 1963, 1965; Chapman, 1966a; Chapman and Bjornn, 1969), by fish species (Hartman, 1965; Ruggles, 1966; Allen, 1969; Chapman and Bjornn, 1969; Lewis, 1969; Pearson, Conover and Sams, 1970), and by fish size (Butler and Hawthorne, 1968; Allen, 1969; Chapman and Bjornn, 1969). In addition, definitions of what constitutes cover and how it is to be measured are neither clear nor consistent to the degree that comparable results have been obtained (Delisle and Eliason, 1961).

It is not the purpose of this report to provide a review of literature outlining the general value of shelter to fish populations. The fact that improvements in shelter typically increase the carrying capacity of streams, especially for larger fish, is fairly well documented. This review attempts primarily to point out articles and findings that may refer to interactions existing between streamflow and cover.

#### Overhead Shelter

Streambank vegetation can control erosion, influence stream temperatures and influence the supply of terrestrial plant and

animal matter that enters the stream. Along with undercut banks and other overhanging objects, it provides areas of shade preferred by many fish such as brown trout, brook trout, Salvelinus fontinalis, and rainbow trout (Newman, 1956; Wickham, 1967; Butler and Hawthorne, 1968; Baldes and Vincent, 1969; Chapman and Bjornn, 1969; Lewis, 1969). Overhead cover provides shadow areas along stream margins where water currents are, for small fish, frequently optimal for resting. Moderate reductions in flow could rapidly diminish the amounts of vegetative canopy and undercut banks in some streams (Butler and Hawthorne, 1968; Idaho Water Resources Board, 1969), thereby reducing the amount of suitable habitat and productivity of the stream, and thus its carrying capacity for fish.

Hartman (1963) states that there is an increase in the association of brown trout with shade cover and low velocity water in summer that serves primarily for efficient feeding. There is more feeding activity and less hiding among stones at this season than in winter, a pattern that also appears to exist for rainbow trout and coho salmon. Hartman also notes reduced association with stream substrate in the spring. Hartman (1965), Chapman (1966a), Allen (1969), Mundie (1969), and Everest and Chapman (1972) report that smaller fish utilize the slower water along the margins of larger streams. Though the majority of drift organisms escape these fish, terrestrial food items, cover, and preferred depths and velocities are gained along shorelines. The importance of the stream margin is indicated by Mundie in his outline of an ideal food channel for maximum coho smolt production. The majority

of features -- shallow depth, numerous marginal back eddies, copious overhanging vegetation, and banks permitting hiding places -- are all tied to the accessibility of this area to fish.

There is evidence, too, that young coho may avoid areas of very dense shade (Ruggles, 1966; Chapman and Bjornn, 1969; Pearson, Conover and Sams, 1970). Pearson, et al., suggest that overhead canopy which encloses more than 90 percent of the available sky may exceed an optimal level. As an example of species differences, brown trout apparently utilize overhead cover to a greater degree than do rainbow trout (Butler and Hawthorne, 1968; Lewis, 1969).

Only one study appeared in the literature in which the influence of discharge on the amount of overhead cover in a natural stream channel was actually quantified. On Blacktail Creek, Montana, Kraft (1968) mapped overhanging vegetation and undercut banks, and discovered that flow reductions of 25 to 75 percent resulted in cover losses that exceeded 36 percent in only one of six test areas, where the loss was 54 percent. Kraft (1968, 1972) reported that at 90 percent flow reduction cover loss ranged from 39 to 56 percent. At the highest level of dewatering, the total amount of cover lost was greater in riffles than in pools. In this study, the conclusions of Wipperman (1969) and Kraft (1972) were that overhead cover was not greatly influenced by high levels of dewatering. Their study, however, was made in a well-defined channel, and results may differ elsewhere.

It should also be noted with regard to the interaction between overhead cover and streamflow that in many cases the loss of streambank vegetation can alter the annual streamflow regime. Meehan, Farr, Bishop and Patric (1969) summarized findings of a wide range of studies which demonstrated that removal of mature stands of trees or other vegetation along streams increases the summer supply of water. They report that initial increases in water yield, considered independently of other factors, appear roughly proportional to the percent of the fully developed stand that is removed. Corning (1969), however, reported that reductions in vegetative canopy through grazing brought about higher and shorter-term winter flood peaks and lower summer streamflows. In Corning's study, compaction of the soil through grazing may have reduced its moisture-holding capacity, which led to lower summer minimums.

Though the general value of overhead cover to fish is recognized, it is evident that much remains to be learned about the interrelationships between streamflow and this form of cover, including associated factors such as water temperature, fish species preferences and terrestrial food sources. Streamside vegetation is clearly important to small as well as large fish. Additional studies under more controlled conditions will likely be required to determine cover needs by fish species, fish size and season. Research of the type reported by Kraft and by Wipperman, where more specific effects of flow on cover are

measured and related to fish populations, needs additional repetition. Whether or not the results of their work are typical also needs further confirmation.

### Submerged Shelter

The great importance of stream substrate and other submerged material as forms of cover for salmonids has been widely demonstrated. It is noteworthy that much of the valuable knowledge gained regarding ties between salmonids and the stream bottom has come from detailed behavioral studies not especially designed to indicate the value of substrate as shelter. The relationship between stream fish populations and the substrate is complex, involving much more than simply the provision of hiding places in the event of predator attack. Later in this report the importance of stream substrate in the production of fish food organisms will also be considered.

At lower levels of flow in most stream channels any increase or decrease in discharge substantially alters the area covered by water and, potentially, the amount of submerged cover. Submerged shelter, then, is a subject of particular interest in terms of the effects of flow on the carrying capacity of streams.

### Use by small fish

From the very earliest free-swimming life stage on, the importance of submerged objects to salmonids is apparent. Small salmonids

recently emerged from the spawning gravel frequently hide under stones, often in shallow riffles (Hoar, Keenleyside and Goodall, 1957; Hartman, 1965). Hartman states that submerged objects are important as reference points, and Kalleberg (1958) and Baldes (1968) show conclusively that small individuals habitually using a specific area are always associated with some form of submerged structure or object. Allen (1969) also notes that shelter within a fish's territory is essential. Kalleberg states that in his stream aquaria, fry defending territories took shelter among stones when larger parr passed by. The pattern of activity operated so well that for days fry could occupy smaller territories within the territory of a larger fish. Baldes found in his studies in an artificial channel that fish did not occupy areas devoid of cover, even where suitable water velocities existed. Other authors noting the value of stream substrate as a form of shelter included Neave (1958), Wickham (1967), and Pearson, Conover and Sams (1970).

#### Seasonal and diurnal use

Submerged cover may assume different values or levels of importance seasonally. Stream substrate is of considerable importance in winter as refuge from the scouring effect of freshets (Hartman, 1965; Chapman, 1966a; Chapman and Bjornn, 1969), and for predator avoidance due perhaps to loss of leaf canopy (Hartman, 1963; 1965). Hartman (1963) notes that increased association with the stream bottom in winter is probably also related to reduced

feeding activity. Hunt (1969) believed that increases in a trout population after habitat improvement (including cover manipulation) were largely the result of increased overwinter survival.

Hartman (1963) states that increased feeding activity on a more abundant food supply in summer may result in a reduction in the degree of association with the stream bottom. He also notes that there are some general similarities in summer and winter patterns among rainbow trout, brown trout and coho salmon, although the present review indicates that notable species differences do exist in the use of submerged cover. Since the abundance of food drift (see section on invertebrates) is greater at higher water velocities, the summer distribution of fish such as juvenile chinook salmon and steelhead trout is usually closer to high velocity water (Chapman and Bjornn, 1969).

Diurnal variations in the use of submerged cover have also been demonstrated for several species. Allen (1969) reports that at night, with a loss of visual orientation, young coho salmon sink to the stream bottom to avoid downstream displacement. He notes, however, that the pattern may differ for smolts undertaking seaward migrations. Chapman and Bjornn (1969) found that young chinook salmon and steelhead trout also settled to the bottom at night, generally after moving inshore, and that there was also increased riffle occupancy at night. Newman (1956) observed that brook and rainbow trout moved out of pools in the evening, apparently to shallower water, and returned the next day. Kalleberg (1958)

regularly observed Atlantic salmon, Salmo salar, and brown trout fry resting at night in fissures between stones.

#### Species differences

Requirements for submerged cover, perhaps partly the result of behavioral interactions, are known to vary by species as well as between salmon and trout groups. Younger age groups of trout species along the West coast are generally stationed in riffles or are associated with rubble in shallower water (Hartman, 1965; Chapman and Bjornn, 1969; Everest and Chapman, 1972). Salmon frequently are located in deeper water or in pools (Hartman, 1965; Mason and Chapman, 1965; Everest and Chapman, 1972) and may be associated with substrate particles of smaller size than are trout (Chapman and Bjornn, 1969; Everest and Chapman, 1972). Salmon, correspondingly, have been found to be less associated with larger submerged objects than trout (Hartman, 1965; Ruggles, 1966; Chapman and Bjornn, 1969), and appear to be more surface-oriented (Peterson, 1966; Fraser, 1969). Allen (1969) summarizes studies which he believes indicate that the brown trout is not as closely associated with the bottom as the Atlantic salmon, lying higher in the water and taking more food at the surface.

#### Effect of water velocity on substrate use

Many authors have reported that there is increased association of fish with the stream substrate as current velocity increases

(Lindroth, 1955; Kalleberg, 1958; Hartman, 1963; Baldes, 1968; Everest and Chapman, 1972). Hartman notes that because of friction between water and substrate, velocities are reduced near the stream bottom (Figure 2). In artificial streams, Baldes noted increased dependence of brown trout on channel irregularities with increasing velocity, and Kalleberg observed movement of juvenile brown trout and Atlantic salmon to increasingly sheltered positions. Lindroth reduced water velocities to zero, and observed that young Atlantic salmon left the bottom, formed schools and moved in all directions. Elson (1939) reported similar findings for brook trout. Kalleberg found at zero velocity that slow upstream migration took place.

The degree of substrate irregularity, along with other factors to be discussed later in this report, apparently influences space requirements of fish through the element of visual isolation. Kalleberg (1958), Chapman (1966a) and Allen (1969) all suggest that increased visual isolation can increase density of fish. Chapman believes that in summer, density of most species is regulated by a space-food, and sometimes by a space-shelter mechanism. Kalleberg states that bottom topography, aquatic vegetation, and turbidity have a screening effect that increases visual isolation. He notes that increased association with stream substrate, caused by increased velocities, also brings about visual isolation and perhaps greater density.

There is evidence that submerged objects such as large boulders can at times substitute for overhead cover. Baldes (1968) found,

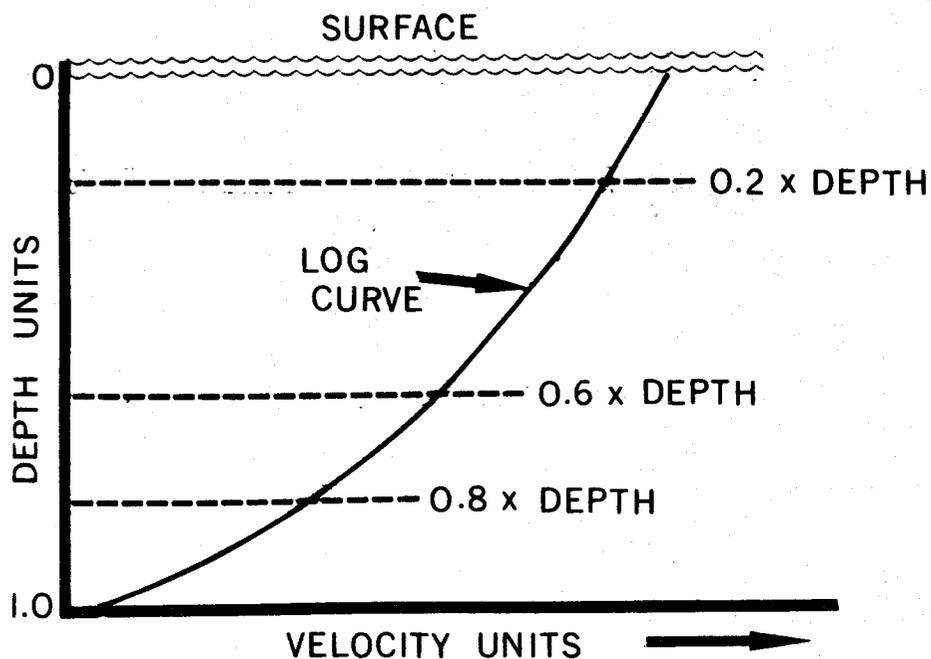


FIGURE 2. Diagram of vertical velocity gradient in a stream channel. The velocity at any one point in the channel is nearly inversely proportional to the logarithm of the depth. Mean speed of flow occurs at about 0.6 of the depth. Mean of speeds of flow at 0.2 and 0.8 of total depth may be used to obtain more accurate mean speed of flow. Steepness of the gradient towards the bottom depends on the roughness of the streambed. (from Hynes, 1970)

for small fish, that a thigmotactic response (one in which a submerged, stationary object is directive) appears to substitute for a lack of overhead cover. For larger fish in larger streams, Chapman and Bjornn (1969) indicate that in the center of the stream, deeper, turbulent water with boulders may substitute for canopy. Burkhard (1967) and Swedberg (1967) have found in stream channelization

studies that the addition of rock jetties and boulders, along with depth increases, apparently aided in maintaining satisfactory trout populations despite removal of streamside vegetation.

Comparatively little is known about the specific requirements of salmonids in terms of substrate particle size. Chapman and Bjornn (1969) point out the obvious correlation between fish size and size of submerged objects. Clearly large fish find little shelter on relatively smooth stream substrates, but small fish may. Most underyearling steelhead in the Chilliwack River, B.C. were found under stones 20 to 40 cm in diameter, according to Hartman (1965).

Aquatic vegetation appears to have considerable value as cover while rooted and after becoming detached (Boussu, 1954). Small fish utilize rooted aquatic vegetation extensively, while fish of all sizes may utilize overhead cover provided by floating mats of aquatic vegetation and other debris. Boussu reported that rooted aquatics appeared to have little effect on the abundance of legal size fish. As stated, Kalleberg (1958) has noted that aquatic plants increase visual isolation through their screening effect. Submerged vegetation also has obvious value to aquatic invertebrates.

The foregoing remarks regarding relationships between salmonids and submerged shelter are intended to point out the intricacy of the problem of determining the cover requirements of stream salmonids, as well as how cover may vary with streamflow. Contrary perhaps to the bases of some recent methods for recommending streamflow

minimums, definition and quantification of this important element of the stream environment cannot be considered simple. This fact will be discussed later in a critique of various methods of determining streamflow recommendations. It is unfortunate that during the study reported by Kraft (1972) an evaluation was not made of the influence of submerged cover under differing levels of flow reduction, particularly to note changes in fish distribution or adjustments related to the availability of different types of shelter. Although a difficult task, such information may be of great value in interpreting observed changes in fish populations at different levels of streamflow.

#### STREAMFLOW AND FISH FOOD ORGANISMS

It is beyond the scope of this report to attempt to fully review the extensive literature on the general ecology of lotic invertebrates important as food for fish. The ecological requirements of stream populations of these organisms are difficult to understand because of the diversity of species, life histories and habitat requirements generally present, yet their role in production of fish makes some consideration here a virtual necessity. A discussion of several of the environmental factors influencing aquatic invertebrates should serve to illuminate possible consequences of streamflow alterations to the fish food resource. In general, stream organisms are separated for this discussion into bottom-dwelling and drift groups, and drift further separated into aquatic and terrestrial components.

## Physical Factors Influencing Food Supply

### Water current

Water current may generally be of greater and more direct importance to the survival of many stream invertebrates than to salmonids. Species adapted to swift-water environments have been shown by a number of authors to possess rather specific velocity requirements (Cummins, 1966). Scott (1958), in a study of the relationships between trichopteran larvae and substrate type, concluded that the most important parameter in determining distribution patterns was current velocity. Allen (1959) arrived at a similar conclusion for aquatic invertebrates in general. Elliott (1967b) stated that variations in water velocity appeared to have little effect on numbers of organisms in the benthos, but his gross measurements of surface velocities may have been inadequate in demonstrating relationships.

Bottom-dwelling invertebrates (benthos) live in a vertically-constricted boundary layer (Prandtl's layer) between the water mass and the stream substrate. Velocity of current in a water course decreases rapidly nearer the substrate (Figure 2), and at sub-microscopic distances theoretically becomes almost zero (Leopold and Maddock, 1953; Ruttner, 1953). Current velocity is of primary importance to the fauna through the rate of oxygen renewal in the boundary layer (Ambuhl, 1959). The stronger the natural stream currents, the less prominent are free-swimming forms and the greater the dependence of the existing fauna on water current for

respiration (Ruttner, 1953; Ambuhl, 1959). Eriksen (1966) states that currents provided by natural water flow are of perhaps greater significance to respiration than the oxygen content of the water itself. Still-water forms typically create their own currents for respiration through movements of the body or body parts (Ruttner, 1953), but nymphs adapted to clinging in swifter water are forced to swim and may die under conditions of substantially reduced water velocity (Ambuhl, 1959; Elliott, 1967a). Currents also facilitate colonization of new or previously dry stream channels (Elliott, 1967a; Waters, 1969), and some species depend on currents to supply food (Sprules, 1947).

Ruttner (1953) states that the influence of water current is manifested in the quantity of organisms produced per unit area. This statement is based on the fact that increasing water velocity brings about a greater exchange between the organism and its water supply, promoting more respiration and food acquisition. Physiologically, then, moving water is richer in oxygen and nutrients than still water. Eriksen (1966), in a more recent view, feels that the significance of Ruttner's concept lies not in the idea that flowing water is important because it is physiologically richer, but rather that current renews the respiratory environment of forms that do not in themselves possess apparatus or behavior to produce a similar effect. Ruttner's viewpoint implies that reduced currents might result largely in lessened productivity of the benthic community, while Eriksen's emphasizes the greater danger of significant mortality among members of the community.

That reduced current limits the abundance and diversity of swift-water invertebrates has been demonstrated by Sprules (1947), Briggs (1948) and Trotzky (1971), but the reductions in these studies may not be attributable entirely to lesser "physiological enrichment" or death, since sedimentation or other changes influencing the amount of habitat likely had occurred. Of course, excessive velocity that scours the stream substrate through molar action can be extremely detrimental to benthos as well (Surber, 1936, 1951; Tarzwell, 1937; Sprules, 1947; Briggs, 1948; Elliott, 1967a; Kennedy, 1967).

Current thus can strongly affect the types and distribution of benthos on the stream substrate, and this conclusion has been reached by Sprules (1947), Needham and Usinger (1956), Scott (1958), Ambuhl (1959), and Egglshaw (1964). There are limited data which demonstrate that, in general, the greatest numbers of organisms can be found in riffles at intermediate velocities (as measured in open water) ranging from 1.0 foot per second (fps) to about 2.5 fps (Table 1), although definition of velocity sampling sites was not always clear. Kennedy's (1967) data indicate peak kinds, numbers, volumes, and weights at velocities of 1.0 to 1.2 fps in riffle areas. Few invertebrates were present in his samples at the lowest recorded velocity of 0.5 fps. Ruggles (1966) found the standing crop of benthos in a shallow, artificial channel flowing at 1.2 fps to be 10 times greater than in an intermediate depth channel flowing at 0.6 fps. Pearson, et al. (1970) report peak invertebrate

numbers at velocities of about 2.0 fps. Surber's (1951) data suggested a broader range of optimal flows, but are somewhat inconclusive. Kelley, Cordone and Delisle (1960) and Delisle and Eliason (1961) suggest that the common insects utilized by trout as food in California are rare where current velocities are less than 0.5 fps or more than 3.0 fps.

In a list of guidelines for recommending rearing flows for salmonids in Oregon, Thompson (1972) specifies riffle velocities of 1.0 to 1.5 fps. Delisle and Eliason (1961) define food-producing areas in California as those where current velocity near the bottom is 0.5 to 3.0 fps. It would appear from the present information that "open water" velocities near 0.5 fps are too marginal, and that an ideal range would be from about 1.0 to 2.0 fps. Depth and substrate are of course important, interrelated factors that should also be considered along with velocity. Severe limitations may be placed on these velocity data, however, as discussed in the section on sampling problems.

TABLE 1. Relationship between water velocity in stream riffles and numbers of bottom organisms in three studies.

Current velocity (fps)	Number of organisms		
	Pearson, et al. (1970)	Surber (1951)	Kennedy (1967)
0.5 - 1.0	53	99	444
1.1 - 1.5	90	148	881
1.6 - 2.0	120	115	484
2.1 - 2.5	89	152	289
2.6 - 3.0	105	125	171
3.1 - 3.5	65	339	-
3.6 - 4.0	62	-	-

/1 Surber recorded surface velocity; depth of measurement not specified in other studies.

/2 Inadequate sample size.

### Water depth

Depth in natural stream channels is normally inextricably tied with velocity, substrate, and perhaps importantly with other environmental features such as distance from the shoreline, and its separate effect on invertebrates does not appear to be fully understood. Depth is believed by several authors to be important in productivity, but explanations of why this might be are usually lacking. One hypothesis is given by Needham (1934), who reasons that photosynthetic production of invertebrate foods (microscopic phytoplankton) depends on light intensity, which in turn depends on depth. Photosynthetic production of algae or other insect foods might have greater significance in areas with little streamside vegetation, where dependence on allochthonic energy sources is not so great.

While some genera of invertebrates are located in deeper (swifter) water, the bulk prefer shallower areas according to Needham and Usinger (1956). Kennedy (1967) reported that the majority of bottom organisms were found in depths ranging from 3 to 6 inches, and that numbers decreased at greater depths. The productive, artificial channel described by Ruggles (1966) was 6 inches deep.

### Importance of substrate

Stream substrate, also fundamentally inseparable from velocity (Sprules, 1947), is considered to be of major importance to stream

invertebrates (Needham, 1934; Linduska, 1942; Smith and Moyle, 1944; Sprules, 1947; Ruttner, 1953; Cummings, 1966; Thorup, 1966; Kennedy, 1967; Corning, 1969). According to Linduska, bottom type appeared to be more important than surface velocity in limiting distribution of organisms. Smith and Moyle reported that the physical nature of the bottom was the most important single factor influencing production of bottom fauna in streams. Thorup stated that substrate type appeared to be the most helpful environmental characteristic in delimiting biotopes of bottom fauna. In a study of the effects of water level fluctuations on trout streams, Corning concluded that benthos production in free-flowing sections of stream was not directly related to low flow conditions, but to streambed materials. Of the three major environmental factors (velocity, depth, substrate), Kennedy concluded that substrate material was most important in influencing the distribution and abundance of bottom organisms.

Sprules (1947) postulated that there is a direct relationship between the useable surface area of stream bottom particles and the productivity of aquatic insects, and Scott (1966) attempted quantification of a cover concept in the benthic environment. In an experimental design based on substrate size and spacing in a natural stream, Scott found a significant positive regression of total numbers of organisms on increasing substrate surface area. Needham and Usinger (1956) found low correlations between organisms and substrate type, but the substrate of the one riffle they examined was relatively uniform.

According to Ambuhl (1959), the boundary layers of reduced flow around stationary objects in lotic environments serve as protective spaces for stone-dwelling fauna (Figure 3). Elliott (1967a) reports that lotic benthos is generally strongly thigmotactic, attached to stones for the most part, especially in daylight. Kennedy (1967) reported that late summer growth of algae on substrate materials reduced the area to which organisms could attach and thereby lowered their abundance. Substrate material has also been noted as a form of shelter for benthic fauna by Sprules (1947) and Egglshaw (1964). The relationship may be similar in some ways to that between juvenile salmonids and the substrate.

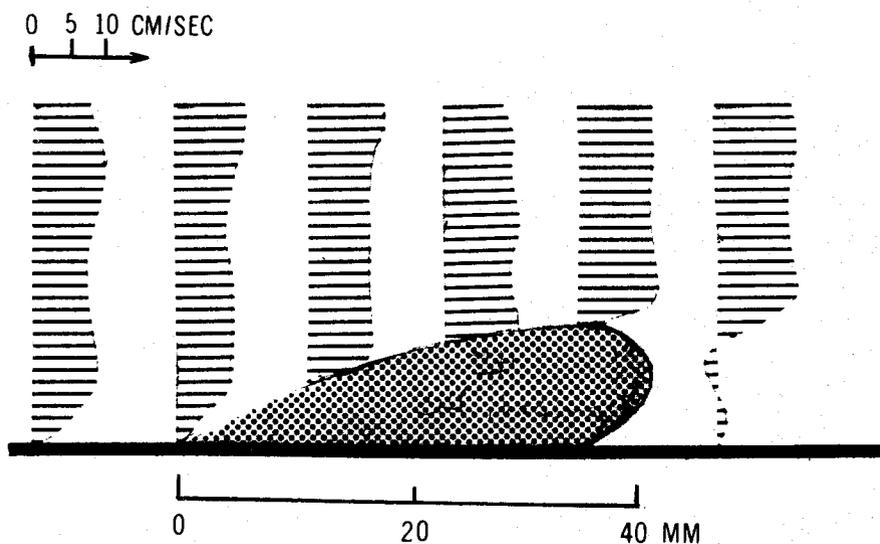


FIGURE 3. Representation of vertical water velocities from surface to substrate (adapted from Ambuhl, 1959). Pattern shown in relation to 40 mm stone lying on smooth substrate.

Under natural stream conditions "rubble" is usually considered the most productive type of substrate (Needham, 1934; Pennak and Van Gerpen, 1947; Sprules, 1947; Delisle and Eliason, 1961). Pennak and Van Gerpen noted decreasing standing crops of benthos in the series rubble-bedrock-gravel-sand, while Kennedy (1967) reported decreases through the series medium rocks-small rocks-large rocks-sand-boulders-silt. Sprules found a decreasing gradient of insect emergence over substrates composed of rubble-gravel-muck-sand. Tarzwell (1936) and Idyll (1943) found that bottoms supporting aquatic plants (with resulting large amounts of surface area) were highly productive, and Idyll believed mud bottom to be more productive than rubble. In general, however, the diversity of available cover for bottom fauna appears to decrease as the size of inert substrate particles decreases (Sprules, 1947).

Cummins (1966) concluded in earlier work that substrate particle size can serve as a common denominator in the benthic ecology of lotic waters. In terms of specific substrate sizes, Kennedy (1967) found that the majority of organisms preferred substrate composed of rocks 2.6 to 7 inches in diameter. Areas with small rocks were less productive because they failed to provide habitat for the larger insect species. Delisle and Eliason (1961) defined food-producing areas as those having large gravel over two inches in diameter, or rubble. Clearly more specific information is needed on relationships between substrate size and invertebrates.

In actuality, substrate is to a degree a product of water velocity (Eriksen, 1966). Moon (1939) notes that in rapidly flowing

(erosional) water, all but the coarse substrate units are washed away, while in regions of reduced current (depositional) finer particles and sediments are deposited. In uncontrolled streams, high flow periods largely determine distribution of substrate in the channel.

#### Stream size

Although Corning (1969) reported that overall production of benthic invertebrates in a stream was reduced in accordance with reductions in wetted surface area, there is evidence that the relationship between stream size and abundance of organisms is not linear. Small streams with shallow depths and moderate velocities are usually quite productive. Jenkins (1970) found that between 10 and 65 organisms (mean 38) drifted past a sampling point hourly in a snow-melt rivulet discharging less than 0.08 cubic feet per second (cfs). Briggs (1948) reported that relatively slight flows of two cubic feet per second or less are sufficient to maintain a fairly rich bottom fauna. One criterion of an ideal food channel, according to Mundie (1969), is narrow width. Progressive declines in the general abundance of invertebrates between the shoreline and mid-stream areas have been demonstrated in larger streams by Needham (1934) and Needham and Usinger (1956). Wider streams appear thus to be less productive per unit area than narrower streams, depending primarily on current velocity and depth.

### Light intensity

Elliott (1967a, 1967b) and Waters (1969) report a strong negative phototaxis among aquatic invertebrates, where light intensity governs the degree of activity. These authors and Chapman and Demory (1963) state that benthic organisms generally remain under stones in daylight hours, but at night they actively move about the substrate foraging. Night activity apparently gives rise to the commonly observed increases in drifting organisms observed at reduced light intensity. Jenkins (1970) observed that moonlit nights inhibited the activity level of insects and reduced the feeding success of fish. Light intensity apparently also governs the diurnal pattern of emergence in many insect species (Sprules, 1947). Some lesser numbers of organisms have been found, in contrast, to be day-active, and for these temperature (Waters, 1969) or light intensity (Elliott, 1967b) may be the controlling factor.

### Gradient

Stream gradient is also tied to other factors including velocity and depth, and is generally not considered as a factor influencing invertebrates. Ruttner (1953) notes that the number of species in the course of a river decreases with increasing gradient. Sprules (1947) demonstrates a differential linear distribution of insects in stream riffles related to distance from the stream source that is associated primarily with changes in average water temperature. In steep, cascading stream channels with high velocities, insects highly adapted to torrential conditions may be found.

## Biotic Factors Influencing Food Supply

### Food of invertebrates

Literature is too extensive to permit discussion of the entire food chain of salmonid populations, but some pertinent comments regarding the foods of stream insects should be noted. Most stream invertebrates feed on plant detritus (Surber, 1951; Egglshaw, 1964; Mundie, 1969), on its associated microflora (Egglshaw, 1964) or on algae (Ruttner, 1953). A relatively small percentage are carnivorous. According to Cummins (1966), primary production is predominantly by periphytic algae in erosional (swift-water) habitats, while in depositional areas, detritus of allochthonous and autochthonous origin forms the major base of food chains. Egglshaw (1964), however, reports the presence of substantial amounts of leaf litter in riffles as well. Both Cummins and Egglshaw remark on the influence of water currents in distributing allochthonic plant materials along the streambed.

Perhaps most important is the degree to which introduced plant material (such as leaf fall) contributes to the energy source of stream invertebrates. In several stream areas the contribution of terrestrial leaves to the total plant energy ingested by aquatic insects has been shown to be from 50 to nearly 100 percent (Nelson and Scott, 1962; Chapman, 1966b; Minshall, 1967). Clearly, adjacent vegetation is extremely important in supplying energy to many stream systems.

### Vegetation

Kennedy (1967) reported that shade from shoreline vegetation apparently had little effect on the distribution of bottom fauna in the stream he studied. If light intensity and temperature largely govern aquatic drift, it seems logical that dense canopy vegetation could influence diel drift periodicities to some extent.

Aquatic plants do provide food and suitable habitat for many stream invertebrates, and areas containing such vegetation can be highly productive (Tarzwell, 1936; Idyll, 1943). Elliott (1967a) also suggests that aquatic vegetation may serve as a "sieve", and check to some degree the movement of drifting organisms.

### General seasonal considerations

As briefly mentioned, there are seasonal elements in consideration of the effects of streamflows on invertebrate populations that are brought on by climatic factors, life history patterns, and other causes. Pennak and Van Gerpen (1947) and Kennedy (1967) reported wide numerical variations for insect groups in bottom samples seasonally, concluding these were due chiefly to the seasonal course of the life histories of various species. These seasonal differences should be understood for various geographical regions in order to accurately assess the potential consequences of streamflow changes to invertebrate fauna. Life history factors of importance include time of egg deposition and hatching, rate of development, and time of emergence from the water. These subjects, except for brief mention, will not be discussed in detail in this report.

Most observers note an apparent summer abundance of stream bottom, emerging and terrestrial insects. Though many stages are active or prominent in this season, substantial populations of benthic fauna are present as well in streams throughout the winter (Needham, 1934; Briggs, 1948). Neill (1938) and Delisle and Eliason (1961) note that many invertebrates need from one to three years to reach adult or reproductive stages, the former authors stating that for this reason year-round habitat is a requirement for maximal production.

Peak abundance of bottom fauna has been reported to occur in March (Briggs, 1948), May (Needham, 1934), August to October (Surber, 1951), October to April (Ellis and Gowing, 1957) and October to June (Kennedy, 1967), indicating the extent of variability among streams. Pennak and Van Gerpen (1947) found no annual variation in abundance of bottom organisms in a Colorado stream. Insect emergence occurs in the spring and summer (Surber, 1951; Elliott, 1967a), and according to Muttkowski (1925), Surber (1951), and Ellis and Gowing (1957) may lead to temporarily reduced levels of abundance of bottom organisms.

Chapman (1966b) concluded for an Oregon stream that aquatics were less available (as drift) in the fall than at other seasons, and suggested that this might have been caused partly by relatively stable (low?) streamflows that were not conducive to dislodging benthic fauna. Regularly declining summer flows in this region could be presumed to have just this effect, perhaps in this manner resulting in increased dependence of salmonids on terrestrial forms for food.

### Invertebrate Drift

Insect drift is a normal feature of lotic systems (Chapman, 1966a; Elliott, 1967a, 1967b) that is intimately associated with streamflow and is of considerable importance to salmonids as a source of food. An excellent paper by Waters (1969) discusses invertebrate drift and its significance to fish.

It was noted earlier that most benthic invertebrates are negatively phototactic, exhibiting greater activity during periods of darkness or reduced light intensity. A number of studies have also demonstrated increases in drift abundance at night (Chapman, 1966a; Elliott, 1967a, 1967b; Chapman and Bjornn, 1969; Dill, 1969; Everest and Chapman, 1972). Elliott (1967a, 1967b) ties these occurrences together, suggesting that drift density reflects the number of animals moving across the exposed parts of stones and plants and the degree of competition for food and space. Since only a small proportion of the total benthic population enters the drift, he speculates that the organisms do not actively detach but lose their grip or are jostled by others and are then vulnerable to being swept away by water currents. His explanation is supported by the fact that drifting insects are generally local in origin, and appear to reattach to the substrate soon after displacement, often in pools where currents are decreased (Elliott, 1967a; Waters, 1969). Additional support is provided by Elliott (1967b) who found that the density of individual species in the drift was apparently highest during periods of rapid growth when competition for food and space

may have been most severe. In contrast to passive displacement, emerging insects apparently do actively detach from the substrate in swift water areas (Neill, 1938).

Waters (1969) believed that drift was a function of production rate, perhaps after the carrying capacity of the substrate was reached, and acted as a means of removal of excess production during nymphal growth. He concluded that diel periodicities in drift were the result of circadian activity rhythms entrained by the cyclic environmental factors, since the rhythms persisted for short periods in the laboratory under noncyclic conditions of continuous light or dark. Waters' remarks do not seem to conflict with Elliott's general premise that drift is a passive event occasioned by the combination of activity patterns and water currents.

Minshall and Winger (1968), in a limited study in a small stream (50 cm wide), concluded in contrast that drift was an active process under conditions of reduced water velocity and depth, resulting in reversal of the normal avoidance response to light. Their findings appear to conflict with other studies of invertebrate behavior and of the effects of water velocity.

The bulk of the preceding discussion suggests the likelihood of a strong positive correlation between current velocity (or stream discharge) and the quantity of aquatic drift, and most authors have shown this to be the case (Chapman, 1966a; Elliott, 1967a; Mundie, 1969; Waters, 1969; Everest and Chapman, 1972). Waters states that current velocity is the major factor affecting the magni-

tude of aquatic drift, and that increasing velocities should increase drift up to the point of catastrophic conditions. He further suggests that abnormal (high) velocities may have a great effect on drift at times when the organisms are active and drift is normally high, but a negligible effect at other times. Elliott (1967b) states that drift abundance depends on water velocity and night length, and presents equations describing the relationships.

Everest and Chapman (1972) found in limited sampling that drift nets set in velocities of 2.6 fps produced twice as many invertebrates in 15-minute periods, in daylight and at night, as nets set in velocities of 1.3 fps. Elliott (1967a) presents data which also suggest that drift rate, or density, is relatively constant over short periods of time. The relationship between flow and drift in Elliott's study was not linear between months, however, indicating that factors such as life history may seasonally modify the effect of current.

Dependent on geographical latitude or other factors, drift is usually greatest in summer (warm months) and least in winter (Chapman and Bjornn, 1969; Hartman, 1963; and Waters, 1969). In this instance drift is probably not casually related to streamflow, but perhaps to seasonal factors such as temperature, periods of emergence, or invertebrate feeding habits. Elliott (1967a) and Waters (1969) report that certain species, including some Baetis and Ephemera, demonstrate increased drift at very low levels of current velocity. In these situations the organisms are probably,

through movement, creating their own currents for adequate respiration, an occurrence that may be uncommon under natural stream conditions except during severe drought, etc. Waters suggests that such drift might also serve to displace organisms to sites of more rapid current. Velocities in the study reported by Minshall and Winger (1968), however, did not appear sufficiently low for this type of activity to take place.

Elliott (1967a) concluded in one study that there was no correlation between the density of benthos and the quantity of organic drift, a surprising finding considering his statements that drift was partly a reflection of competition between animals for food and space and that some organisms may be dislodged through contact with others. If the latter statements were true, some correlation between benthos density and drift, although possibly slight, would seemingly be present. Reimers (1957) reported that major drift groups were set adrift in rough proportion to their abundance on the stream bottom, and Dimond (1967) also found evidence which suggested that drift is a density-related occurrence. Elliott's data may have been influenced by additional factors which masked such a relationship.

Although drift is chiefly aquatic in origin, terrestrial insects may at times be a significant component (Chapman, 1965; Elliott, 1967a). Terrestrials that enter the stream may remain a part of the drift for extended distances.

As final points of possible interest, Everest and Chapman (1972) found no correlation between water velocity and size of drifting

invertebrates in limited sampling in two streams. They found in one stream, however, that organisms drifting in daylight were significantly smaller than those drifting at night. No explanation was offered for this occurrence. Elliott (1967a) reported that of the benthic fauna, only larvae in stony cases were not represented in the drift.

### Riffle Productivity

Riffle areas of streams deserve separate mention because of their recognized importance in the production of invertebrate fauna. It is a widely accepted belief that riffles, with depths, water velocities, and substrates that provide optimal environments for the majority of invertebrate species, are much more productive than lentic areas (Pennak and Van Gerpen, 1947; Sprules, 1947; Ruttner, 1953; Briggs, 1958; Kelley, Cordone and Delisle, 1960; Delisle and Eliason, 1961; Ruggles, 1966; Pearson, Conover and Sams, 1970). Both Needham (1934) and Briggs (1948) reported that 80 percent of the benthos production in their study streams occurred in riffle areas. Tarzwell (1937), however, found that only 51 and 56 percent of the production occurred in riffles in two Arizona streams. Idyll (1943), considering all benthic species (including large clams), believed pools to be more productive than riffles.

In a viewpoint that differed from that of Ruttner (1953) mentioned earlier, Sprules (1947) suggested that the high productivity of rapids, where the bottom is often composed of rocks and

rubble, is related to the variety of microhabitat types (more so than current) available to various species of invertebrates. He stated that the size and configuration of substrate particles determines the amount of shelter available for insect species with differing body sizes. Information regarding substrate type was discussed earlier in this section.

In a study of coho salmon production, Pearson, Conover and Sams (1970) found that pools with larger riffles upstream averaged higher in coho production per unit of pool area than pools with small riffles, evidence that food production in riffles may be quite important to fish. A stream composed entirely of riffle would conceivably permit the greatest amount of invertebrate production, but would provide little habitat for fish.

#### Significance of Terrestrial Insect Fauna

Terrestrial invertebrates commonly enter streams by falling from nearby vegetation, or may be washed in from shoreline areas by wave action or fluctuating water levels (Mundie, 1969; Fisher and LaVoy, 1972). Once in the stream the organisms become a part of the food drift, and may be extensively used by fish (Surber, 1936; Kelley, Cordone and Delisle, 1960; Delisle and Eliason, 1961; Kennedy, 1967; Allen, 1969).

Elliott (1967a) found that terrestrial organisms at times dominated the surface drift of insects for brief periods of less than 24 hours. He reported them to be most abundant in summer months, and

particularly on sunny days. Weather conditions were an important determinant of their occurrence. Mundie (1969) noted that terrestrials in Turtle Creek, British Columbia, were most abundant in the second half of summer.

Ants, flies, grasshoppers and beetles were mentioned by both Surber (1936, 1951) and Kennedy (1967) as terrestrial items. Other groups comprising the terrestrial drift included spiders, leafhoppers, crickets, bees, butterflies, moths and lepidopteran larvae.

#### Streamflow Conditions Influencing Summer Food Supply

##### Reduced streamflow

Two studies directly concerned with the influence of streamflow reductions on aquatic invertebrates were located, one assessing effects on benthic populations and one examining drift. McClay (1968) studied effects of controlled flow reductions on physical characteristics and benthic invertebrates in one riffle of a Montana stream. He found that reductions influenced water depth and velocity most, and stream width and surface area least. At 90 percent dewatering, velocity decreased 74 percent, while surface area decreased only 32 percent. The stream meandered through a well-defined channel, however, and base flows appeared to be substantial. At 75 percent dewatering, overall insect densities in an unaltered (control) riffle increased while those in the dewatered riffle remained stable. Densities in the dewatered riffle relative to those in the natural flow riffle, however, were significantly higher

during the period of reduced flow than during an earlier full-flow period. McClay suggested the higher densities may have resulted from settling out of drift organisms under reduced flow, or emigration from exposed areas. Increases brought about by emigration, however, have been reported as short-term by Corning (1969). During the period of 90 percent dewatering, fewer differences between control and dewatered riffles were observed, but the results were not conclusive because of other problems.

In a study of the effect of reduced streamflow on invertebrate drift, Minshall and Winger (1968) reported increased drift under reduced discharge. Their results, based on sampling in a 50-cm wide stream, differ from those of a number of other studies on the effects of velocity on drift. Additional investigation on this topic would seem an important future objective, as would further examination of the effects of reduced summer streamflows on benthic insects.

#### Fluctuating and controlled flows

A significant amount of information on the effects of fluctuating flows on aquatic invertebrates exists, but little seems to be known about the long-term influence of controlled (stable) flows. Several authors have documented the alternate stranding, desiccation and flushing of insect fauna that commonly takes place below hydroelectric installations (Briggs, 1948; Powell, 1958; Thompson, 1970; Fisher and LaVoy, 1972). Such water conditions generally cause sub-

stantial reductions in production and standing crops of bottom fauna (Powell, 1958; Runnstrom, 1960). Sprules (1947) notes that only the most tolerant species are able to complete their life cycles in intermittent streams subjected to drying and other influences, a statement which probably applies to natural as well as man-caused fluctuations. The flushing effect of freshets or other extreme fluctuations in flow is most severely felt by free-roving immature stages of insects and groups such as Ephemeropterans, Plecopterans and Chironomids, while attached larvae and groups such as Trichoptera and Simuliidae may be little affected (Sprules, 1947).

There is evidence that with recession of flow lateral migration of some benthic groups such as Plecoptera and Ephemeroptera can occur (Sprules, 1947; Corning, 1969), but concentrations of organisms caused by such conditions appear to be short-term.

Fisher and LaVoy (1972) found benthic invertebrates to be adversely affected by periodic exposure caused by fluctuating water levels below a hydroelectric dam. They offered an interesting comparison between tidal fluctuations in seashore areas and the man-caused fluctuations below dams. They reasoned that since a freshwater "intertidal" condition is a recent artifact of man's activities, insufficient time had elapsed to allow evolution of complex and productive communities such as exist in saltwater. The detrimental influence of water level changes, according to the authors, was heightened by the fact that normally productive shallow water habitats were essentially lost under conditions of fluctuating water levels.

Tarzwell (1937) and Hourston (1958) suggest that stable streams having low ratios between high and low flows are generally productive. In support of this generalization it has been abundantly shown that highly fluctuating flows can be very destructive to benthic organisms. In addition, Briggs (1948) reported that bottom fauna production was greater under controlled flow conditions below a dam, concluding that effects were beneficial. There may be some question, however, as to whether a positive relationship between flow stability and aquatic productivity is altogether true for relatively static flows over extended periods, especially for invertebrate populations. Although Briggs found overall increases in numbers of bottom organisms below the dam, the composition (and perhaps food quality?) of the fauna was definitely altered. Production of mayflies and stoneflies, which contribute substantially to the aquatic drift utilized by salmonids, was much lower below the dam, while production of caddis-flies increased greatly. Such qualitative changes, regardless of biomass considerations, could be very important through their influence on fish populations.

The change in invertebrate population structure below the dam as reported by Briggs appeared to have been caused by deposition of sand and silt in riffles and other areas, with a corresponding loss of substrate surfaces used by insect groups such as Ephemeroptera and Plecoptera. In an analogous situation, Eustis and Hillen (1954) reported severe changes in benthic organisms caused by sedimentation below Granby Dam, Colorado. Scheduled releases failed to carry

away sediment, and a large-scale flushing operation was necessary to achieve at least partial sediment removal.

### Sedimentation

The list of publications concerning the effects of sedimentation of stream invertebrates is lengthy. For those interested, good reviews of literature on this topic are provided in Cordone and Kelley (1961) and Gebhardt (1969). These authors summarize findings of other studies which indicate clearly the harmful effects of suspended sediments and streambed silting. It appears fairly certain from the literature that sedimentation largely influences rearing fish in an indirect manner through reduction of their food supply. The principal mode of invertebrate reduction appears to be through loss of habitat caused by the accumulation of silt among and over substrate particles.

Sedimentation problems are often visualized as those brought on by severe streambed or land disturbance and erosion. In natural streams sedimentation from these sources might not be long-term problems since, through periods of high streamflow and streambed scouring, productive substrate materials such as rubble and gravel can be re-exposed. In controlled streams with more stable flows, however, some sedimenting activities may continue, and unless the substrate is "cleansed" periodically long-term sedimentation and loss of invertebrate habitat seems a likely possibility (Eustis and Hillen, 1954).

### Sampling Problems in Invertebrate Studies

Because of typically large sample variability, much of what has been learned regarding the influence of stream physical factors on invertebrate populations is of a qualitative nature. The problem of obtaining quantitative information on invertebrate numbers or production has been discussed by a number of authors, including Surber (1936), Allen (1941), and Elliott (1967b). Needham and Usinger (1956) best indicate the high level of sampling required for reliable quantitative data. Weber (1966) conducted multiple linear regression analyses between numbers of benthic organisms and many physical and habitat factors, and found no useable, statistically significant relationships. He also concluded that sample variability may have been a major reason for the lack of significant correlations. Elliott (1967b) discovered that some species were rare in bottom samples, but not in the drift, and later found these organisms to be located in specific habitats not adequately sampled with the techniques used. Ellis and Gowing (1957) found their samples to be influenced by the fact that breeding populations of Asellus intermedius migrated laterally within the stream in late spring.

Clearly many factors affect the abundance of bottom organisms, and apparently combine to render low-intensity sampling of little value in understanding relationships or estimating production. Besides the three important topics of water velocity, depth, and substrate type, other factors that come to mind are water temperature, oxygen content, seasonal changes, and invertebrate food supplies.

In estimating production, Allen (1941) and Pennak and Van Gerpen (1947) emphasize the need for obtaining adequate samples from all substrate types and for calculating the proportions of these substrate types comprising the total stream bottom. Waters (1962) presents a potentially valuable method of estimating, from the drift, the production rate of stream invertebrates. The possible usefulness of this approach in overcoming some of the problems inherent in sampling benthic populations makes further testing desirable.

The usefulness of many sampling techniques and types of equipment appears also to be open to considerable question, according to Ambuhl (1959) and Eriksen (1966). These authors state that gross measurements of the stream environment are of little value to the understanding of the microenvironment, and Eriksen makes a strong plea for determination of parameters within the microhabitats of given organisms. He notes that the fallacy of only measuring current on the surface, in the middle, or in some place in the water column presents serious problems, and the inability of many studies to result in conclusive findings seems to bear this out. In measuring velocities, Eriksen suggests that devices such as pitot tubes, Gurley current meters, and float methods are of little value in studying microhabitats of benthic organisms, and that even midget or pygmy current meters taking measurements 2 to 3 centimeters from the bottom may be unsuitable for microdistributional studies. Apparently adequate tools for some of the most needed measurements in lotic ecology are still unavailable.

### General Conclusions Regarding Invertebrates

Production of stream invertebrates, the principal salmonid food supply, depends on many factors. Over a range of geographical areas invertebrate production in streams differs, depending upon such factors as stream physical characteristics and chemical properties and the amounts of autochthonous and allochthonous organic material present as food for invertebrates. Relatively little is known, however, about the food requirements of stream insects at different stages in their life histories. Within individual streams, current velocity and substrate appear to be the major governing forces in production. In light of the importance of invertebrates as food for fish, the effects of streamflows on stream invertebrates may be as important as any other element of salmonid ecology.

Much additional research is required to define relationships between water velocity or streamflow and invertebrate production. Work accomplished thus far has experienced unexplainable variability and lacked conclusiveness because the many factors involved have not been adequately considered, or because the techniques used were inadequate. Meaningful study of the influence of water current could require consideration of depth, current patterns, velocity gradient between surface and substrate, inter-substrate currents, substrate type and size, abundance of detritus, and other factors for each sample taken. Seasonal, species, and other differences must be understood. More specific information on the effects of currents on invertebrate drift is also needed.

With continued proliferation of dams and the increased potential for flow manipulation, assessments of the influence of more constant streamflow regimes on qualitative and long-term changes in invertebrate populations are needed. Considering the importance of substrate type in providing habitat for benthic organisms, any change that tends to increase sedimentation or in other ways reduce habitat may have great significance in the productivity of the stream system.

It would also be of considerable value to understand the relationship between shoreline vegetation and the supplies of plant materials and terrestrial insects entering the stream, as these sources of energy are of obvious importance. Chapman (1966b) reported unpublished research at Oregon State University which indicated that reduced canopy vegetation tended to increase the importance of aquatic organisms in the diet of cutthroat trout. Very dense canopy may have some influence as well on the density of aquatic invertebrates in the drift.

#### SALMONID FEEDING BEHAVIOR

The relationship between salmonid feeding behavior and the food supply is an important aspect in production, and again is a topic importantly associated with water currents. Feeding behavior has been extensively studied, and it would be difficult to summarize all the information available or to improve upon the excellent discussions prepared by such authors as Chapman (1966a), Allen (1969), Chapman and Bjornn (1969), Mundie (1969) and Waters (1969). It is

hoped that a discussion here will serve mainly to emphasize the significance of some of the relationships between environmental characteristics, such as streamflow, and salmonid feeding behavior. It should be remembered before discussing these relationships that feeding activity, as with the use of shelter, is for territorial fish such as salmonids often closely related to the regular use of small parts of the available habitat within streams.

#### Feeding and Water Current

Young trout and salmon normally obtain food from the drift, from the benthic fauna, or via cannibalism and predation on other fish (Chapman, 1966a; Allen, 1969). Chapman notes that salmonids most likely cannot subsist on benthos available within their territories, so must rely heavily on incoming organic drift.

Water currents influence the feeding of salmonids on invertebrate organisms in two important ways. First, moving organisms visually stimulate fish and cause feeding to take place (Chapman, 1966a). Drift is more visible, therefore more available (Waters, 1969). According to Chapman, benthic prey must move on the stream bottom to be attacked, and movement is the obvious characteristic of drift. Secondly, as has been discussed, the quantity of invertebrate drift passing a given point in a unit of time depends on water velocity. The significance of these relationships is great. An increase in food supply and availability accompanying higher water velocities could reduce the amount of stream area required

to obtain adequate food, and thereby increase the stream's carrying capacity for fish (Chapman, 1966a; Pearson, Conover and Sams, 1970). The data of Mason and Chapman (1965) and Peterson (1966) also suggest that the level of drift is a factor determining carrying capacity.

As was previously discussed with regard to shelter requirements, small fish tend to utilize stream margins and move into deeper, swifter water as they grow. Smaller fish are probably more susceptible to transportation by currents, thus water velocities may be most important in restricting their distribution. As size increases, fish are able to move further into the stream and take advantage of more abundant drift resources. Individuals in these instances do not attempt to maintain positions facing the strong currents that carry organic drift, but lie nearby in areas of moderated velocity created by substrate irregularities (Chapman and Bjornn, 1969). Laboratory studies have also suggested that the distribution of fish within a channel is associated with feeding opportunity (Mason and Chapman, 1965; Chapman and Bjornn, 1969) and this has led Chapman and Bjornn to believe that much of the underlying reason for positive correlations between fish size and selection of higher velocity water is food supply. These authors note, however, that so far it has not been possible to assess the relative importance of food supply versus cover provided by depth and turbulence (and larger substrate material?) in causing fish movement to faster, deeper water. Seasonal differences introduce an additional compli-

cating factor. Hartman (1963) suggests that summer association with certain environmental features may serve primarily for efficient feeding, while winter associations may emphasize shelter.

Allen (1969) speculates that since growth is influenced by the amount of energy expended to obtain food, and more foraging may be required to obtain adequate food at reduced flows, there is a potential for reduced growth in slower currents. This concept seems appropriate for salmonids that depend to a considerable extent on drift resources, but it may not have been documented through field or laboratory studies. Observations in artificial channels by Ruggles (1966) support the idea of increased energy expenditure at reduced flows. He found that in swifter water young coho salmon maintained position and fed efficiently on the incoming drift, but that in slower water fish actively swam about chasing food items such as terrestrial insects. Reimers (1957) states that trout in sheltered pools in winter are not required to expend much energy to maintain position. Although currents may be greatly reduced under pool conditions, feeding is probably at a low ebb and fish are therefore relatively inactive. If the relationship described by Allen exists, the questions remain as to the conditions of flow that would cause significant changes in drift availability, feeding behavior, or energy expenditure.

#### Diurnal and Seasonal Considerations

Feeding amplitude of salmonids has in general been shown to be much greater during the day than at night. This has been demon-

strated for rainbow trout by Newman (1956) and Jenkins (1970), noted for coho salmon by Mundie (1969), reported for brook trout by Hoar (1942) and Newman (1956), for brown trout by Kalleberg (1958), and for Atlantic salmon by Hoar (1942) and Kalleberg (1958). The governing factor in diurnal feeding is the degree of illumination. When incident illumination drops below a certain level (which might be different for different species) feeding declines. Hoar (1942), Newman (1956) and Kalleberg (1958) found feeding to be somewhat depressed at mid-day, apparently owing to effects of high temperature, or to strong light which could have increased shade-seeking reactions and fright responses. The majority of findings indicate an evening peak in feeding amplitude. Jenkins (1970), however, presents contradictory data showing that feeding amplitude was highest in mid-day in summer and autumn for rainbow trout in California.

Mason (1966) found that young coho salmon fed actively at night, especially under conditions of moonlight. He believed that the high retinal cone sensitivity of coho fry might be of adaptive value in exploiting the diel organic drift cycle. Further research on this subject seems worthwhile, as the general impression gained from other studies is that a poor correlation exists, except perhaps for the evening period, between feeding and drift cycles.

Feeding and food requirements are greatest in the spring and summer (Delisle and Eliason, 1961; Hartman, 1963) and often begin to decline within the summer period (Neill, 1938; Chapman, 1966b; Kennedy, 1967). This latter pattern appears to be the case for at least some

salmonids in Oregon coastal streams, according to Chapman (1966b), Lowry (1966) and Giger (1972). Chapman and Bjornn (1969) summarize studies which indicate most salmonids feed throughout the winter. They suggest that winter foods may be adequate even though drift abundance is generally lower, since digestion rates are lower under winter conditions.

#### Feeding and Invertebrate Drift

Some relationships between salmonid feeding and drift resources were discussed in the section on feeding and water currents. Also, Mason's (1966) comments with regard to the adaptive significance of night feeding by coho on drift appear in the section on diurnal considerations. Chapman and Bjornn (1969) support Mason's view in their general discussion of salmonid feeding behavior. Waters (1969) provides a lengthy discussion indicating the significance of invertebrate drift to stream fish populations. Additional authors noting the importance of drift as a food supply for salmonids include Kalleberg (1958) and Chapman (1966a).

Waters' (1969) discussion is of particular interest. He suggests that the principal direct importance of drifting invertebrates to fish predators lies in an increase in the availability of food. He lists two direct effects of drift on food availability. In one case, drift serves to transport organisms from inaccessible areas (possibly shallow riffles) to places where fish reside (possibly in pools). In the second case, drift carries organisms

to a wider assemblage of fish species with varying microhabitats. Waters notes that although drift is reduced in abundance as it progresses across pools, fish can utilize organisms after they have settled out on the pool bottom (under Chapman's concept of prey movement, however, only organisms that were alive and moved after settling out would be utilized by fish). In terms of evolutionary implications, Waters suggests that drift may indirectly optimize production of invertebrates and maximize fish food supply. He cautions, however, that specific relationships between drift and fish production remain little known.

Kalleberg (1958) and Chapman (1966a) also confer evolutionary significance on the use of drift by stream salmonids, stating that by this means of food acquisition energy is conserved and survival is benefitted, and that through territorial activities the population is spread and food supplies are efficiently utilized. Their statements appear to support the concept of reduced growth with slower currents as presented by Allen (1969). Some of Chapman's other comments are associated with this topic, in which he notes that drift is not as pronounced in pools (where currents are reduced), and that fish in pools tend to exist in loose hierarchies and scramble for food.

It was earlier noted that food drift and feeding cycles appeared in general to be poorly matched. Additional information is supplied by Jenkins (1970), who found that immature aquatic insects were rarely taken by rainbow trout at mid-day when feeding was most

intensive because they were at that time poorly represented in the drift. They were taken frequently, however, during less intensive night feeding. Although moonlight permitted increased feeding, ~~it also reduced drift abundance, and the net result was a reduction~~ in feeding success. This lack of correlation was one of the factors leading Chapman (1966a) to suggest that drift feeders could probably not over-exploit the drift resource.

#### Feeding on Terrestrial Insects

Although the principal food of salmonids throughout the year might consist of aquatic insects, there can at times, particularly in summer, be considerable supplementing of the diet with terrestrial forms (Kalleberg, 1958; Chapman, 1966a; Kennedy, 1967; Allen, 1969; Mundie, 1969). Surber (1951) reports one example of the heavy use of terrestrial fauna by fish in a Virginia stream. He found that from mid-May to mid-June, 66 percent of the diet of rainbow trout and 90 percent of the diet of brook trout was terrestrial fauna. Perhaps of equal significance, Demory (1961) reported for a small Oregon coastal stream that terrestrial invertebrates comprised 30 percent of the diet of small coho salmon on an annual basis. Chapman (1966b) ~~later arrived at the same value for coho, and noted~~ that the addition of a portion of the unidentified component of the diet would increase the terrestrial contribution. In the Oregon stream, greatest use of terrestrials occurred in early July and from mid-August to November. Kennedy (1967) reported that ter-

restrial insects were also an important trout food source between June and November in a California stream, and that overall they constituted approximately 22 percent of the food items in the stomachs of all trout. In the month of October, terrestrials exceeded aquatics by volume in trout stomachs.

Shoreline vegetation largely governs the quantity of terrestrial organisms entering the stream system, thus great differences between streams in the availability of this food source are possible dependent on amounts of canopy vegetation. For example, in a study of trout feeding Neill (1938) purposely selected an area with little streamside vegetation to avoid contribution by terrestrial insects, and was apparently successful since less than one percent of the fish diet was composed of terrestrials. This factor should be taken into consideration when attempting to compare results of various studies.

One reason for dramatic increases in consumption of terrestrial forms during seasons in which they are available might be that their occurrence near the water surface or in the drift, unlike that of aquatic forms, is reasonably well matched to salmonid feeding periods. Warm, sunny days in spring and summer provide conditions for peak activity of flying or crawling insects as well as for substantial feeding by fish. As Jenkins (1970) reported, rainbow trout fed actively at mid-day in summer and autumn, and the majority of food items taken at that time were terrestrial in origin or were adult aquatic forms (the surface floating component of the drift).

Some evidence suggests that substantial feeding on terrestrial insects in summer and fall is not strictly related to their availability but may also be brought about by declining streamflows. Chapman (1966b) reported a decrease in intake of aquatic foods by small coho in the fall, suggesting that relatively stable (low) streamflows were not conducive to dislodging insects and thus contributed to a decrease in availability of drift. Ellis and Gowing (1957) found in comparing two stream areas in summer that the one possessing a higher benthic population held fish that fed consistently on aquatic forms and maintained good condition, while the section with a low benthic population held fish which were in poorer condition and were feeding extensively on terrestrials. They concluded that the use of terrestrials was the result of a paucity of organisms of aquatic origin. The results of these two studies suggest that low, stable flows causing reductions in aquatic drift promote increased feeding on terrestrial forms. Mundie (1969), in support, offers the same explanation for late summer feeding by coho on terrestrials. In a related view, Powell (1958) believed that terrestrial food items helped make up for an impoverished aquatic supply in an area below a dam.

There are other factors to consider as well in interpreting changes in food habits at times of declining streamflows. For example, with declining flows, riffles are reduced in area to a much greater degree than are pools, and fish may be forced to move from shallow areas to pools (Kraft, 1972). Egglisshaw (1967) presents

evidence that the food habits of Atlantic salmon and brown trout residing in pools differ from those of the same fish residing in riffles, terrestrial forms being more pronounced in the stomach of fish in pools. In addition, he found fish to be feeding more at the water surface in pools than in riffles. It is conceivable that shifts in habitat and feeding pattern, along with possible increases in availability of terrestrials in pool areas which are often close to streamside vegetation and contain accumulations of floating drift, may be responsible for some of the increase in consumption of terrestrials under reduced flows. Another result of declining riffle area is loss of habitat which is most productive of benthic insects. Clearly more definitive research is needed to fully explain the replacement of aquatic foods by terrestrial insects in the summer and fall.

The question of selectivity, or preference of fish for certain aquatic or terrestrial organisms, may also be important. Some authors believe terrestrial forms are at times preferred and actively sought by salmonids, which would contribute to their heavy utilization. This topic will be discussed in more detail in a later section.

Sources detailing salmonid feeding on terrestrials of various taxonomic groups include Surber (1936), Chapman (1966b), Mundie (1969), and Jenkins (1970). Gebhardt (1969) cites numerous other studies of salmonid food habits.

### Feeding Differences by Fish Species and Size

Species and size of fish bear consideration in analyzing food requirements or feeding behavior of stream salmonids. Length of freshwater life can be used to point out differing levels of dependence of different species on stream foods. As Neave (1958) and Allen (1969) indicate, chum salmon, with a short freshwater life, feed little or not at all in the stream. Coho salmon live and feed for approximately one year in freshwater at a small size, and steelhead trout for about two years at a greater range of sizes. Cutthroat trout in Oregon spend from 2 to 5 years in the stream before migrating seaward, and may reach lengths of 10 inches or more before smolting (Giger, 1972). Clearly, carrying capacity of streams depends on the combination of species and life histories present.

As other examples of species differences, it was noted earlier that coho salmon, through night feeding, might be better adapted than other salmonids to feeding on drift. Coho have been reported to be drift, rather than benthic, feeders by Mundie (1969), but also to be more surface-oriented and to rely more on floating terrestrial organisms than steelhead (Peterson, 1966; Fraser, 1969). These latter authors reported that steelhead utilized benthic epifauna and aquatic drift more extensively than did coho. If, as it appears, small coho tend more than other species to inhabit pools (Hartman, 1965) and to feed substantially on terrestrial organisms, at least during the day, their degree of evolutionary adaptation toward utilization of the aquatic drift could be less than previously indicated.

Egglishaw (1967) reported that stomachs of Atlantic salmon in pools contained more of some benthic forms and fewer terrestrial organisms than brown trout, and concluded that differences were due to behavior or feeding positions. Allen (1969) summarizes other studies comparing these species' habitat preferences which indicate that the brown trout is not as closely related to the bottom as the salmon, feeding more at the surface and from the drift and less on the bottom. In a Virginia stream, Surber (1951) found that rainbow trout stomachs contained more aquatic forms than brook trout stomachs, also perhaps the result of feeding position or behavior.

With regard to fish size, Kalleberg (1958) reported that fry of Atlantic salmon and brown trout seemed to feed more on benthic organisms than older groups. Horton (1961) found that brown trout, as they grew, consumed greater numbers of terrestrial insects. It is generally agreed that as fish increase in size, they feed on larger organisms if available (Larkin, 1956; Horton, 1961; Egglishaw, 1967; Allen, 1969; Mundie, 1969). Larkin suggested that the inability of growing salmonids to acquire larger organisms could affect growth. Newman (1956) reported that feeding activity in pools revealed a hierarchical relationship where status depended on size. These statements indicate some of the relationships that can exist between feeding behavior and fish size.

### Exploitation of Food Supply

The influence which stream salmonids might exert on invertebrate populations seems not to have been established to any satisfactory degree. Ruggles (1959), Chapman (1966a), and Allen (1969) suggested that stream fish might have an impact on their food supply, but other statements raise some doubt as to whether such an impact actually takes place. Chapman also states that it seems unlikely that drift-feeding fish could over-exploit the drift food resource, particularly allochthonous foods, since much of the drift, emergence and ovipositing activities occurs during periods of reduced feeding. As only a minor portion of the benthic fauna appears in the drift at any one time (Elliott, 1967a), the effect seems even less significant. Kennedy (1967) discusses food supplies and utilization in a California stream, suggesting that fish were apparently not utilizing the benthic resources present to any substantial degree. During the day most organisms are hidden away within the substrate, and would not seem to be readily accessible. Thus, under these conditions and the concept of substantial reliance on drift, it does not seem likely that there could normally be a substantial effect on food sources by stream fish populations.

### Food Preference

Statements regarding the existence of selectivity by fish of certain food types have appeared in many papers. In a number of studies, particularly earlier ones, disparities between benthic samples and fish stomach contents were attributed by investigators

to selection. Most recent views, however, favor availability, or accessibility, as the principal factor governing the types of foods eaten (Neill, 1938; Larkin, 1956; Kalleberg, 1958; LaCren, 1965; Allen, 1969). Neill's comments are useful in pointing out how the habits of particular benthic organisms make them more vulnerable to potential predators. The active seeking of flying terrestrial insects reported by Surber (1936), Kalleberg (1958), Ruggles (1966), and Kennedy (1967) suggests possible preference, but limited aquatic food resources may force such feeding activity. In some respects, however, the utilization of larger organisms that accompanies fish growth is a form of selection.

Certain aquatic organisms or groups of organisms are more severely affected than others by fluctuating flows or greatly reduced water velocities. Loss of food resources through flow changes could vary in severity dependent on the levels of accessibility or preference. Most serious would seem to be the loss of food organisms that are both accessible and preferred. Because of diet flexibility, the next most serious case might be the loss of accessible organisms that are not preferred but are eaten. Of lesser impact would be the loss of food items which might be preferred but are not generally accessible anyway, and finally the loss of items that are neither preferred nor accessible.

## MICROHABITAT SELECTION AND TERRITORIALITY

For animals that typically remain for varying periods in localized and at times discrete parts of their environment, the concepts of home range, territory, and more recently station or micron habitat, have been used to describe or discuss habitat selection and environmental requirements. Viewing habitat characteristics in terms of specific preferences of individual organisms provides a means for explaining observed distributions, sizes, species composition, and population levels. A wide variety of aquatic organisms including fish and many stream invertebrates lend themselves to these approaches. It has been suggested that for salmonids in lotic environments, territories seem to be the rule (Kalleberg, 1958). For these reasons, such approaches should be recognized and utilized as useful to the study of complex stream ecosystems and assessment of the potential for stream environments to support fish.

It will become apparent in the following discussion that relationships commented upon in the sections on shelter and feeding frequently reappear. Obviously the selection by a fish of a particular locality involves many physical and biological factors, all of which should be considered in attempts to understand habitat requirements or estimate carrying capacity of streams.

The section is intended to be a general discussion of salmonid habitat selection, and those interested in more specific discussions of micron habitat preference or territorial behavior are urged to re-

view papers by such authors as Newman (1956), Kalleberg (1958), Hartman (1963, 1965), Wickham (1967), Baldes and Vincent (1969), and others. Kalleberg (1958) and Chapman (1966a) discuss the evolutionary significance of territoriality.

### Space Requirements

Simply stated by Chapman (1966a) and Mundie (1969), more water obviously provides more habitat for fish, and reduced flow results in reduced living area. Larkin (1956) and Chapman (1966a) suggest that space and food may be the most important factors influencing density of fish populations in streams. Chapman supports this view for the spring-summer-fall period, and notes that suitable space may assume a more dominant role in winter. Although only one of a number of interrelated factors influencing density of salmonids, space (or related parameters such as surface area) has shown promise as an environmental characteristic through which a significant portion of the variation in fish populations experienced under different flow conditions might be explained. This section attempts to summarize knowledge regarding space requirements of salmonids, how space interacts with other habitat features, and how rigid or limiting space might be in controlling density of fish. If space is of major significance, then low flow periods may determine the numbers of young reaching migrant stage.

Some of the more significant general papers dealing with salmonid space requirements in streams are those of Kalleberg (1958),

Chapman (1966a) and Allen (1969). Allen has assembled available records of densities of young salmonids for comparison. His data show a definite and fairly linear relationship between fish size and average area of streambed per fish, the relation corresponding to an average density of about 1.7 grams per square meter ( $\text{g/m}^2$ ). Of added interest, he found that area per fish did not differ significantly for different species of the same size. Limited data indicated that actual territory size also increased in proportion to the weight of fish. The average area of streambed per fish of any given size, however, appeared to be roughly 15 times the size of the territory occupied by a fish of the same size. Allen speculated from the data that 2 to 20 percent of the streambed (in the streams reported) had the right environmental features for the territories of any one category of fish. He indicated that in larger streams, a smaller proportion of the cross-section would provide suitable conditions for young fish, a relationship noted also by Mundie (1969). Allen's findings provide support for the premise that territoriality (space requirements) can determine the maximum density levels of fish in streams.

Kalleberg (1958) felt that the assumption can be made that there exists a permanent lack of suitable space with regard to the size of growing populations, apparently lending his support to arguments that space plays a major role in controlling density. His studies indicated, however, that territories had rather diffuse borders, and he suggested that in uniform habitats where fish are

not in close contact estimation of actual territory size may be impractical.

After examining several California streams, Burns (1971) concluded that only living space variables were correlated significantly with biomass of salmonids. He stated that decreasing availability of living space caused the greatest mortality, with total mortality highest in the summer of lowest streamflow. Apparently there was poor correlation between biomass and several productivity indicators (total dissolved solids, total alkalinity, etc.), although no data on availability of food or shelter were reported.

Mason and Chapman (1965), Chapman (1966a) and Chapman and Bjornn (1969) suggest that spatial demands are not inflexible and that they appear to be mediated by psychological and physiological factors associated with food. Chapman sees spatial isolation in riffles and other competition for space as partial substitutes for direct competition for food, a view that allows for some adjustment of spatial (territorial) requirements. Chapman and Bjornn discuss aquaria feeding experiments that indicate fish can take advantage of temporary food abundance, subordinating any minimal space requirement to do so. Chapman further states that density regulation may sometimes be through a space-shelter, as well as space-food, mechanism. He suggests, however, that the mediatory effects of food and cover are probably limited, and that there may exist some spatial minimum. Chapman (1965) earlier suggested the possibility that spatial requirements regulate density below ceilings imposed by food supply in a

given year. LeCren (1965) and McFadden (1969) support the views that fish can modify density and that food influences territory size.

Pearson, Conover and Sams (1970), in attempts to correlate coho abundance with spatial parameters, found that pool area was directly related to the numbers of fish in the pool. They discovered, however, that total stream area was even more closely related to coho numbers in pools. This finding indicated the importance of riffle areas, presumably from the standpoint of food supply, and appeared to offer an example of interaction between food and space. Lewis (1969) reported higher densities of rainbow and brown trout in pools with greater current velocities, another example where increased food drift may have been responsible for fish increases.

The foregoing concepts seem important in attempting to estimate or interpret the impact of moderate increases in summer stream discharge on fish populations. As noted previously, flow increases exert a much greater influence on water velocity, and to a lesser degree on riffle area, than on pool area. If set spatial demands strongly regulate pool density, then in many populations of salmonids there may be little benefit derived from substantial increases in discharge. It would seem more logical to accept the view of Chapman (1965) that spatial requirements control density below ceilings set by the food supply. Under these conditions increases in flow could increase density through greater production and drift of food, or through improved microhabitat or shelter conditions leading to increased visual isolation, for example. It would seem

possible to significantly increase the carrying capacity of pools with only slight areal increases. This being the case, pool area would then be a less effective correlate with fish biomass.

#### Influence of Water Current

Literature on stream salmonids clearly demonstrates that current velocity is an important factor in habitat selection and in spatial interactions between fish. Chapman (1966a) stated that habitat differentiation was usually on the basis of water velocity and shelter and a number of authors have noted the influence of current on territorial behavior. Salmonids respond to currents by orienting in the direction of flow (positive rheotaxis), as noted by MacKinnon and Hoar (1953) and Baldes (1968). In general terms, velocity at the focal point or station of a salmonid in the stream must be sufficient for the fish to maintain orientation but not too high to maintain position (Baldes, 1968). At greatly reduced velocities fish are forced to cruise to maintain stability in open water (Elson, 1939; Lindroth, 1955; Ruggles, 1966).

A microhabitat is defined by Baldes and Vincent (1969) as the physical conditions immediately surrounding an animal at a given time and place. They regard the microhabitat as the smallest areal segment of the stream ecosystem, and Baldes (1968) suggests that the number and diversity of microhabitats is directly proportional to the potential carrying capacity for fish. Recent efforts have been made to define the character of microhabitats of different

species of salmonids, most frequently in terms of current velocity and depth but also in terms of nearby physical features such as substrate size and surface, bottom or lateral velocities. Table 2 summarizes microhabitat data found in the literature, some from measurements in artificial channels and some from natural streams. Available data are sketchy and notably variable, and it would be difficult to make reliable generalizations regarding microhabitat velocity preference based on present information. Because habitat selection is highly related to fish size, data such as that reported by Everest and Chapman (1972) are needed where physical parameters are correlated with relatively narrow fish size distributions.

Most areas of suitable velocity for microhabitats are located near the substrate (Baldes, 1968; Everest and Chapman, 1972). As velocities increase, fish move nearer the substrate and are increasingly dependent on channel irregularities to supply areas which can be used as focal points (Kalleberg, 1958; Hartman, 1963; Everest and Chapman, 1972). Thus substrate is an integral part of habitat selection in stronger currents (Figure 4). Velocity becomes less important in controlling use of habitat as streamflow declines in late summer (Chapman and Bjornn, 1969).

In a broader context of habitat use, it has been widely recognized that water current induces territoriality among salmonids (Newman, 1956; Kalleberg, 1958; Hartman, 1963; Mason and Chapman, 1965; Ruggles, 1966; Everest and Chapman, 1972). Newman, in aquaria experiments, found that without currents hierarchies of fish formed

TABLE 2. Depth and velocity characteristics of salmonid microhabitats.

Species	Age	Length (mm)	Depth (m)	Velocity (m/sec)	Reference
Steelhead trout	0	32	<.15	<.15	Everest and Chapman (1972)
	1	95	.60-.75	.15-.30	Everest and Chapman (1972)
	0, 1(?)	varied	.18-.67	.06-.49	Thompson (1972)
Chinook salmon	0	62	.15-.30	<.15	Everest and Chapman (1972)
	0(?)	-	.30-1.22	.06-.24	Thompson (1972)
Coho salmon	0(?)	66-89	-	.09-.21	Pearson, et al (1970)
	0(?)	-	.30-1.22	.06-.24	Thompson (1972)
Cutthroat trout	0, 1, 2(?)	varied	.40-1.22	.06-.49	Thompson (1972)
Brown trout	-	213	-	.12-.21	Baldes and Vincent (1969)
Brook trout	-	200	-	.10 (mean)	Wickham (1967)

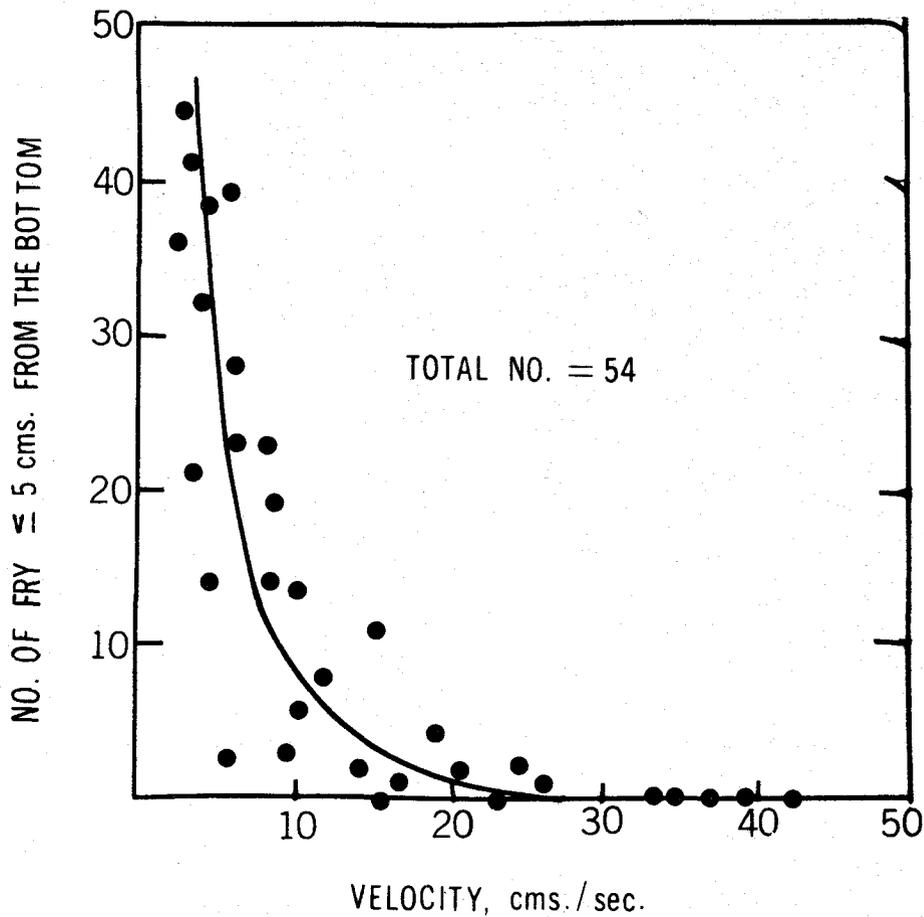


FIGURE 4. Number of Atlantic salmon fry in free water in relation to velocity of current (from Kalleberg, 1958).

and no territoriality was exhibited, even with substrate present that could serve as cover for fish. Similar behavior is frequently observed in pools of natural streams (Chapman, 1966a). In currents fish are better able to maintain a fixed position and obtain food from the drift, but under such conditions frequently find it necessary to defend a site or be displaced by another fish seeking to acquire habitat. It has also been suggested by Kalleberg (1958) and Hartman (1965) that species may differ in the way in which

their aggressive behavior is influenced by water velocity.

It was previously suggested in this paper that increases in densities of fish in pools under increased velocities (reported by Lewis, 1969), might be to some degree the result of greater food drift and perhaps also of improved aquatic shelter through visual isolation or some other mechanisms, rather than strictly space-related. Based on microhabitat selection and the apparent advantages of territorial behavior, populations of fish seemingly could also be benefitted by higher pool velocities through more efficient distribution, as well as through reduced need to expend energy to maintain orientation and acquire food. Growth of fish then, as well as numbers, may be altered by the effect which current velocity has on habitat requirements. Allen (1969), as noted, suggested that increased foraging in slower currents could lead to reduced growth.

Elson (1939) discovered some time ago that fish reacted to changes (increase or decrease) in current strength by temporary increases in levels of activity, the reaction being greater the longer the period of stable conditions prior to change. It seems clear that substantial changes in current velocity would have a highly disruptive influence on territorial behavior and the location of stations or focal points, bringing about increased activity as fish adjusted to the new conditions. The necessity for adjustments and corresponding activity increases, if frequent, might significantly influence growth and perhaps even survival. These consequences appear to be realistic under conditions such as fluctuating discharge below hydro-electric installations.

### Influence of Water Depth

Chapman (1966a) stated that habitat differentiation was rarely on the basis of depth directly, but usually on velocity, turbulence and cover. Everest and Chapman (1972) found that steelhead and chinook lengths correlated significantly with depth, but that microhabitat velocities were apparently of greater significance in controlling distribution. The species differences observed by these authors in depths utilized by steelhead and chinook (Table 2) were discounted in their statement that strictly equal sized fish selected similar depths.

### Shelter and Food Aspects of Microhabitats

Although the value of shelter to stream salmonids has been discussed, it should be noted here as well that cover, whatever the type, is an important aspect of microhabitat selection. Baldes and Vincent (1969), among others, have noted the strong positive thigmotactic response of salmonids, where stationary objects have a major directive influence. They reported that fish in their experimental channels were not found in areas devoid of cover, even though suitable velocities and depths occurred. Others noting that microhabitats are almost always associated with cover include Kalleberg (1958), Hartman (1963, 1965) and Wickham (1967). Kalleberg observed, however, that larger stream salmonids frequently darted from mid-stream stations to shoreline cover when disturbed. His comments suggest that for some larger fish, ideal food and cover con-

ditions may not occur in or immediately near the same microhabitat or focal point.

Food source must influence microhabitat location and perhaps microhabitat characteristics for small as well as for large salmonids. That stations or focal points are usually located near drift resources, and serve as positions from which feeding excursions take place, has been widely noted (Elson, 1939; Newman, 1956; Kalleberg, 1958; Mason and Chapman, 1965; Chapman, 1966a; Chapman and Bjornn, 1969; Everest and Chapman, 1972).

#### Species Behavior and Interaction

There appear, at least superficially, to be differences among species in habitat preference, but this topic requires further clarification. Some differences in shelter use were discussed in an earlier section of this report, but the differences may not in many instances represent true habitat preference. As examples of apparent habitat selection, brown trout have been found to occupy shallower water than Atlantic salmon (Lindroth, 1955), and steelhead trout to occupy shallower water than coho salmon (Hartman, 1965; Pearson, Conover and Sams, 1970). Pearson, et al. suggested that differences might be explained through variation in environmental preferences, steelhead selecting riffles and coho pools. It has also been reported, however, that brown trout are dominant over Atlantic salmon (Lindroth, 1955; Kalleberg, 1958; LeCren, 1965) and that steelhead are dominant over coho salmon (Hartman, 1965; Fraser,

1969). Lindroth speculated that riffles (shallows) were preferred by both brown trout and Atlantic salmon, but that the dominance of browns forced the salmon into other habitats. Hartman, in contrast, speculated that pools were preferred by both steelhead and coho, suggesting that steelhead were found in riffles because they were comparatively more territorial (dominant) in riffles than in pools. Everest and Chapman concluded that if steelhead and chinook of equal size occurred simultaneously they would seek nearly identical habitat conditions. The relatively minor habitat differences they observed were the result of size disparities caused by different times of emergence. Certainly the data in Table 2 do not at this point firmly suggest disparate velocity preferences. The weight of current information seems to favor the idea that substantial differences in habitat preference among species are not common. Some question remains, however, as to whether observed distributions are the result largely of behavioral interaction or of perhaps seemingly unimportant size differences.

#### Fish Size and Habitat Selection

Previous discussion points to the fact that fish size influences selection of habitat. Small fish cannot maintain position in stronger currents, and large fish experience reduced food supply in slower currents and find little shelter in shallows or over smooth substrates. Everest and Chapman (1972) reported that steelhead and chinook lengths correlated significantly with focal point velocity and depth, further

supporting earlier statements that fish move to faster, deeper water as they grow. Hartman (1965) reported that recently emerged steelhead and coho occupied three general habitats: shallow water in small bays on stream margins; shallow, small riffles; and small crevices near inshore portions of logjams and large boulders. Saunders and Smith (1962) found fingerling brook trout primarily in riffles, whereas older fish were found where hiding places such as boulders, submerged trees and stumps, and undercut banks occurred. Territory size, too, is dependent in part on fish size (Kalleberg, 1958).

Since fish as they grow move to faster, deeper water, and since the proportion of shallow, slow-moving water increases significantly under reduced flows (Kraft, 1968), it might be hypothesized that flow reductions would be most detrimental to habitats of species that rear in streams to the largest size. This could be true were streams to conform to a pattern of extreme linearity and correspondingly uniform cross-sectional shape, where deeper, central channel areas with shelter would be lost. The meandering course of streams, however, tends to create deeper pools with undercut banks, submerged objects, and other cover for larger fish that does not appear to be severely affected by low streamflows. Water velocity in pool areas would be lowered under reduced flows, and alteration of food drift, temperature, and oxygen levels could also occur.

### Diurnal Considerations

One other aspect of habitat selection that should be taken into account in determining preferences is that of diurnal variability. Night distribution of fish has been found to differ from distribution in daylight, juvenile fish often moving inshore, into shallower riffle areas, or closer to the substrate during periods of darkness (Kalleberg, 1958; Mason, 1966; Allen, 1969; Chapman and Bjornn, 1969). Chapman and Bjornn suggest that large differences among species in diurnal needs are possible, and speculate further that the suitability of night-station habitat may even be a factor influencing density of fish in the stream environment. For obvious reasons present microhabitat knowledge is based on daytime observations, but examination of diurnal variation appears necessary to fully define habitat requirements.

### STREAM HYDROLOGY

The importance of hydrological study to the understanding of stream ecosystems and development of flow recommendations for aquatic life is obviously great. It seems evident that much of the prospect for broad, ready application of criteria and techniques developed to quantitatively estimate the effects of streamflow on salmonid production will depend on advancements that have been and will be made in the realm of hydrology. A considerable number of current water studies are concerned with hydrological modelling of watersheds,

streamflow simulation studies, stream classification studies, streamflow forecasting, streamflow prediction on ungaged streams, and water quality simulation. In the Northwest, for example, progress is being made in the area of low flow prediction in streams (Campbell, 1971; Orsborn, 1973). These and other subjects are of considerable potential value to further development or application of methods for establishing streamflow recommendations.

Hydrological concepts, except for this brief discussion and in instances where pertinently applied to biological data in the literature, have been omitted for the most part from this review. These warrant extensive consideration at such time that a methodology for broad application of flow criteria is being developed. The reader interested in this aspect of stream dynamics is referred to the many hydrological texts and papers available. New research on many of the above subjects is summarized in project descriptions appearing in the Water Resources Research Catalogs.

#### Hydraulic Geometry of Streams

Leopold and Maddock's (1953) paper on the hydraulic geometry of stream channels is a valuable reference indicating quantitative relationships that exist between stream discharge and such hydraulic factors as depth, width and velocity, and how these are influenced by channel shape, gradient and bed roughness. Hydraulic characteristics of stream discharge strongly influence the aquatic biota as has been shown, and it seems reasonable that, once optimum hydraulic

conditions for biota are known, morphometric measurements of stream channels could supply information needed to calculate the discharges required to provide desired fish and invertebrate habitat. The work of Collings, Smith and Higgins (1970) reported later is an example of the use of morphometric studies in establishing stream-flow recommendations. Such advancement would be greatly benefitted by improvement in the coincident collection of hydrological and biological data and improvement in the degree of interchange between hydrologists and biologists.

#### Importance of Water Velocity as a Hydraulic Factor

This report has clearly indicated the importance of water velocity to stream fish populations. Water current is receiving increasing recognition as an important factor in the needs of all forms of aquatic life (Ambuhl, 1959; Fraser, 1970). This is understandable, since over the centuries stream-dwelling animals have become highly adapted to life in currents (Ruttner, 1953) and presumably are dependent upon them. Changes in stream environments will surely affect the well-being of many inhabitants.

We have seen that current velocity affects juvenile salmonids in many ways. Velocity directly influences aggressiveness and territoriality. It may mechanically force fish to other locations. Perhaps most importantly, it acts on the food supply, affecting both benthic populations of insects and drift abundance. These and other relationships between currents and aquatic animals have

been discussed in some detail in this report.

Hill and Burkhard (1967) report that as the rate of discharge of a stream is reduced, water velocity is influenced to the greatest degree, followed by volume, depth and lastly surface area. In measurements of stream pools, Pearson, Conover and Sams (1970) also found velocity to be most affected by discharge, followed in order by cross-sectional area, depth and width. Other authors have also shown that velocity is proportionately more affected by changes in discharge level than are other hydraulic characteristics (Leopold and Maddock, 1953; Curtis, 1959; Wipperman, 1968; Elser, 1972; Kraft, 1972).

Velocity obviously should receive consideration in attempts to relate stream discharge and production of fish. Limited information on velocity preferences of stream invertebrates and salmonids has been collected, but measurements of currents have frequently been inadequate for useful comparison with biological populations. Stream current systems are extremely complex, involving as one example, the very important velocity gradient extending from surface to substrate that is influenced to a considerable extent by bed roughness. Investigators have attempted to relate gross open water measurements of currents to benthic organisms, but have given virtually no consideration to conditions existing within the substrate habitat occupied by the organisms.

## AGENCY APPROACHES TO STREAMFLOW RECOMMENDATIONS

### Early Approaches

Until recently, streamflows recommended to sustain fish populations have almost universally been judgment decisions based on general knowledge of the life history of fish species and the suspected influence of various levels of discharge on different life stages. Photographic records or other data documenting general conditions at different levels of discharge have frequently been used to establish recommended flows. The U.S. Fish and Wildlife Service has made use of this approach (Anonymous, 1964a, b; 1969) in their efforts to maintain fisheries in tailwaters below dams. Idaho's streamflow recommendations are another example of an approach based largely on judgment (Idaho Water Resources Board, 1969). All agencies responsible for setting flow levels for rearing fish still must depend to varying degrees on general concepts regarding fish requirements rather than on specific data.

### California's Proposal

In California, Kelley, Cordone and Delisle (1960) proposed investigations that would determine amounts of water needed to protect trout fisheries below water development projects. Their plan was to quantify the amounts of food producing, shelter, and spawning area present in streams at different flows, and from this information recommend flows that would maintain or enhance fish populations. A field study indicating the potential value of this

proposal was conducted on the Middle Fork Feather River by Delisle and Eliason (1961). Measurements of trout habitat were made at 15 different flows in four different stream sections, and the agreement of the measurements indicated that the method could be successfully applied (Figure 5). Unfortunately, the earlier proposal for large-scale development and implementation of the ideas on many California streams has apparently never been realized. The techniques presented meshed important biological factors such as food production and cover with streamflow in a logical fashion. Present methodology in California was not clarified through recent contacts (G. E. Delisle and D. R. Hooper, personal communication), suggesting that a firm program is not in effect at this time.

#### Oregon Wildlife Commission

Earlier recommendations by the Oregon Wildlife Commission of flows for fish rearing were based largely on observations of flows and judgment. As greater familiarity with biological requirements was gained, methods became increasingly detailed. The progression of these efforts can be seen in the long series of Basin (later Environmental) Investigations reports published by the Wildlife Commission, more recent examples of which are Thompson and Fortune (1970) and Smith and Lauman (1972). Currently, a combination of physical measurements (depths, velocities, etc.), general observations, and judgment are being used to make rearing flow recommendations. Some of the recommended criteria were presented earlier in this

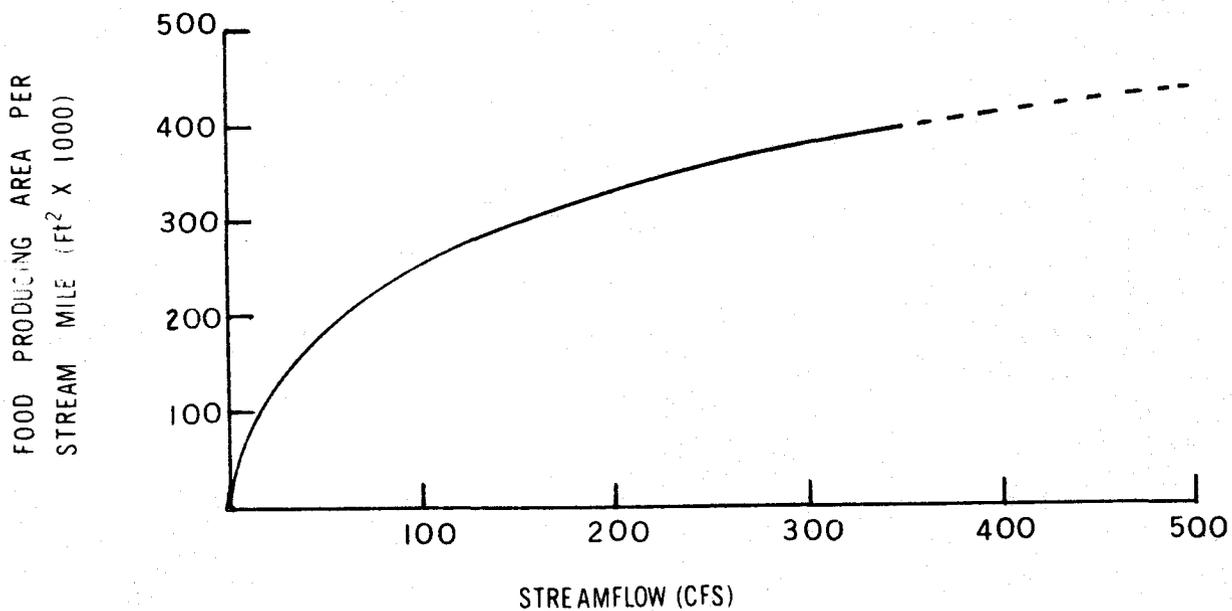
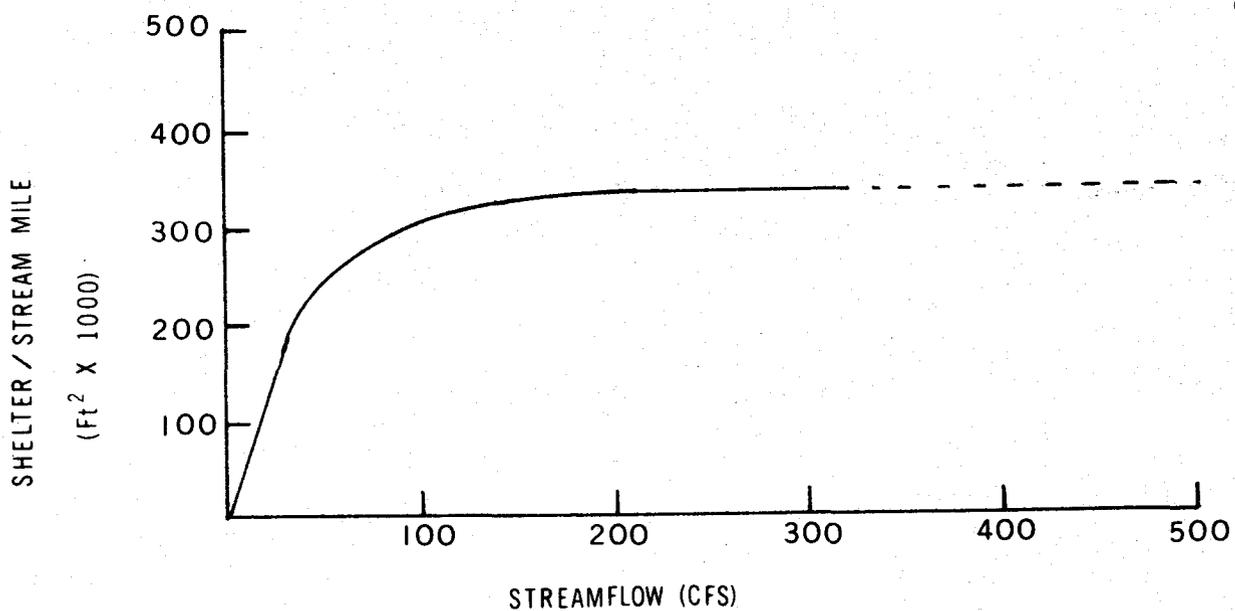


FIGURE 5. Examples of the manner in which fish habitat characteristics (cover and fish food production) are quantified and related to stream discharge to determine optimum flows, Middle Fork Feather River, California (Delisle and Eliason, 1961).

report. The procedures for surveys are lengthy and the reader interested in them is referred to Appendix 1 of Thompson (1972).

In an effort to improve and substantiate future flow recommendations in Oregon, measurements of environmental niches of stream-rearing salmon and trout have recently been obtained for incorporation into the present methodology. Data on microhabitat depths and velocities have been collected in a variety of habitats and for several species of fish. In practice, the streamflows would be determined that provided the maximum amount of usable area of preferred depth and velocity, and these flows would then in most circumstances represent the recommended discharge levels. The data obtained for this "preferred environment" concept have not as yet been fully utilized to determine flow recommendations.

#### Fish Commission of Oregon

The Fish Commission of Oregon studied summer requirements of juvenile coho salmon in a series of streams, to aid in predicting coho production by means of summer flow levels and to improve and justify the setting of summer streamflow minimums (Pearson, Conover and Sams, 1970). From their investigations they felt that there were two workable approaches to the determination of optimum streamflows for coho salmon, one using pool velocity and the other riffle velocity and area as criteria.

The "pool velocity" method resulted from their discovery that the average water velocity through study pools was related to the

numbers of fish per pool area. Ninety percent of the observations made of coho rearing in pools occurred between velocities of 0.3 and 0.7 fps. Assuming that rearing conditions would to a degree improve with higher pool velocities, they selected 0.7 fps as the optimum water velocity. The method, then, consisted of obtaining pool measurements in a particular stream that would permit calculation of average pool velocity at different flow levels. Optimum flow would represent the flow at which average velocity approached 0.7 fps.

The "riffle velocity and area" method is predicated on observations that production of fish food organisms depends on the velocity of water through riffles and riffle size, and that food supply in turn helps govern coho production. Provided velocities through pools are not excessive, the optimum flow for juvenile rearing would be the flow providing the maximum amount of fish food. The coho study indicated that peak insect production in riffles occurred at velocities near two feet per second. An optimum flow for food production, therefore, would be the flow that covers the most riffle yet provides large sections of riffle with velocities near 2.0 fps. For a particular stream, measurements of areas and velocities of a sample of riffles would indicate the most ideal combination.

### United States Geological Survey

A comparatively recent method and program of determining optimum flows for rearing is being pursued in western Washington by the U.S. Geological Survey in cooperation with the Washington Department of Fisheries (Collings, Smith and Higgins, 1970). The approach, which can be termed the "wetted perimeter" method, makes use almost entirely of stream channel characteristics and stream hydraulics in deriving flow recommendations. The technique hinges on the fact that, in typical channels, the perimeter of the average stream reach that is wetted increases rapidly with discharge as the streambed is covered with water. Past a point when the majority of the stream bottom is covered, increases in flow bring about only small increments in wetted perimeter as streamflow approaches bankfull (Figure 6). These breaking points in the relationship between discharge and wetted perimeter are determined by graphing data from several representative reaches of each stream. Along with some consideration of velocities and water quality, the breaking points are assumed to provide optimal discharges for rearing. The program ultimately is aimed at the development of an empirical formula for specifying minimum flows required for fish. Some of the development of this approach is based on an attempt to estimate optimum spawning discharges in California through the use of regression equations (Rantz, 1964).

### United States Forest Service

A procedure for determining minimum streamflow recommendations for fish habitat has been developed for the Utah, Idaho and Wyoming

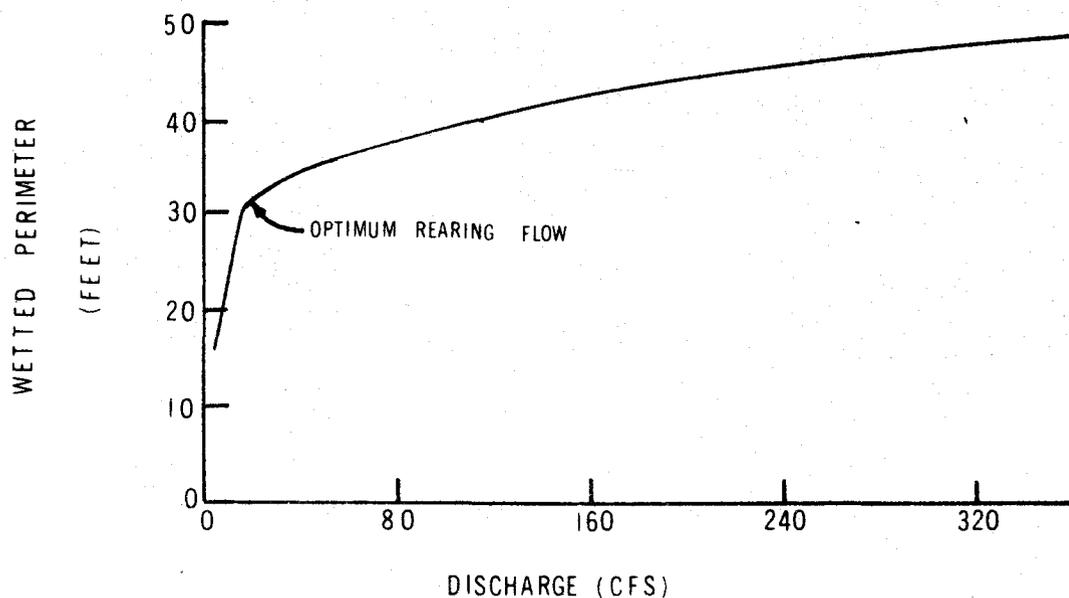


FIGURE 6. Example of the use of the relation between wetted perimeter and discharge to determine optimum rearing flow in a reach of the DeWatto River, Washington (Collings, Smith and Higgins, 1970). The discharge at the point at which the curve changes slope is considered optimum for rearing.

area by the U.S. Forest Service (Chrostowski, 1972; Dunham, 1972). Data used in the determinations are based largely on physical habitat measurements obtained from a series of cross-sectional transects located along a stream course. Observations are made of pool-riffle periodicity, pool quality, stream width, wetted perimeter, water depth, substrate type, streamside cover, bank stability, gradient, and water velocity. Cross-sectional profiles are drawn with the water level at the time of survey apparently serving

as an index discharge. Additional water level lines are drawn on the profiles and resulting changes in habitat estimated from the drawings. Formulae are used to estimate velocities, discharge and a friction index at various flow levels.

The various characteristics measured are grouped in four categories (pool-riffle ratio, pool structure, bottom composition, shelter), and an optimum level (100 percent of optimum) assigned to each. Ratings at different discharge levels are summed and divided by the maximum possible sum (400) to obtain a sample rating. Management recommendations are formulated from the data. Although somewhat difficult to understand from the brief descriptions of methods given, the procedure appears to have some of the basic elements of the "wetted perimeter" and other approaches, although it considers more closely the varied habitat requirements of fish and is, as a result, more complex. Descriptions of some procedures for field measurements are outlined in Herrington and Dunham (1967).

#### Montana Method

In Montana, a relatively simple method for determining minimum streamflows for trout streams has been developed that is reported to be superior to approaches that depend primarily on judgment (Elser, 1972). The method is based on percentages of the mean annual flow of record on individual streams, a 10 percent flow constituting a short-time survival flow and a 30 percent flow a satisfactory fishery flow (Tennant, 1972). Fishery workers in Montana

suggest a 30 percent minimum for the period October-March, and a 60 percent minimum for the period April-September. Any increase, up to flood stage, is considered beneficial to trout fisheries. USGS surface water records supply data needed to perform the calculations, thus implementation on gaged streams can be readily accomplished. Wyoming has apparently also utilized this method extensively on its streams.

#### Recent Trends

In the period since this study was initiated an upsurge of interest in the subject of streamflow requirements of aquatic organisms has been witnessed, an encouraging fact that should lead to an accelerated level of investigation and, consequently, substantial new knowledge. Other reviews pertaining to this subject either have been recently completed (Fraser, 1972; Milton, 1972; Hooper, 1973), or are planned (R. H. Kramer, personal communication). The Pacific Northwest River Basins Commission is currently sponsoring a series of workshops on instream flow requirements through which a number of agencies hope to develop an up-to-date and reasonably uniform methodology for determining flow recommendations. In addition to plans for research in Oregon on summer flow requirements for salmonid rearing, similar, more intensive research may also be initiated in Utah in the near future (R. H. Kramer, personal communication).

## OTHER APPROACHES TO FLOW EFFECTS

Efforts to master the complexities of the stream environment and develop usable techniques for flow evaluation have led to some yet untested points of view in addition to the previously mentioned approaches. Computer simulation modelling is one avenue for dealing with complex aquatic systems that has the potential for being especially applicable to flow determinations. Because of the newness in application of simulation studies to fishery problems, little has been accomplished in this area. There are plans at the present time for large-scale, interdisciplinary modelling and study of streamflow-fish production systems in Utah (R. H. Kramer, personal communication). There also are modelling efforts in progress in some fishery agencies, but none at present are closely related to production of fish in natural streams.

One of the original objectives of this review was to attempt to model streamflow-fish production relationships, incorporate data into the model, and point out where additional research was needed. When it became apparent that data on the subject was rather meager to permit construction of a useful model, emphasis was shifted to design of field studies that would provide new information on streamflow and its relationship with several basic factors of the stream ecosystem (food production, habitat or space, shelter, etc.)

There have been attempts to establish gross relationships between streamflow and salmonid production, with the hope of developing some ability to predict juvenile or adult population levels with little knowledge of biological processes occurring in the stream. Smoker (1953, 1956) presents data that indicates significant correlations between stream discharge (average annual runoff or total runoff in freshwater life stage) and numbers of coho salmon and steelhead trout in western Washington. Smoker (1956) suggested that in certain streams coho and steelhead juveniles find a limiting factor, or complex of factors, in the total volume of streamflow that tends to dominate all other variables.

McKernan, Johnson and Hodges (1950), studying trends in salmon populations on the Oregon coast, found that low summer flows appeared to produce below average adult runs in some streams, whereas higher summer flows appeared to be followed by increases in resultant fish runs. Little relationship was observed between the magnitude of high winter and spring flows and survival to subsequent adult runs, although exceptional winter floods seemed to produce poor resulting runs.

In British Columbia, Wickett (1949), Neave and Wickett (1953) and Neave (1958) demonstrated relationships between minimum summer streamflow and returns of adult coho salmon two years later. Wickett stated that fish numbers depended on the size of the stream during the year of juvenile residence. Henry (1953) makes broad comparisons of minimum flows during incubation and landings of

chum salmon in Tillamook Bay, Oregon, that in general indicate positive correlations.

#### FLOW METHODOLOGY AND SALMONID ECOLOGY

It is difficult and perhaps unfair to attempt to compare or evaluate various methods of determining recommended streamflows based only on a general review of papers describing such methodology and on a perusal of literature on stream ecology. Nevertheless, a discussion pointing out methodology patterns and how these may relate to populations of organisms has value in suggesting areas of further study or modification of approaches. As happens frequently in biological investigation, methods have been diverse and have developed along separate lines, making summarization into reasonably well-defined categories a sizable task.

#### Judgment Approaches

Many judgment approaches to flow recommendations have advanced from earlier, strictly "eyeball" techniques, and many employ some quantitative or measured elements. As knowledge of habitat requirements of fish increases, judgment tends to improve, provided observers have taken advantage of findings by incorporating them into their methods. There may indeed be some truth to the suggestion that many judgment recommendations might later prove comparable to those made through use of the most advanced techniques. Judgment decisions have

a definite advantage over some approaches by being less restrictive in the use of a variety of general biological knowledge in formulating recommendations.

Judgment recommendations are unsatisfactory because they mostly lack interrelated, quantitative elements. Biologists have misgivings regarding their accuracy, and they are usually indefensible under criticism. Visual "appearance" certainly is not an adequate criterion. Another problem, common to all approaches, is the difficulty of melding knowledge regarding requirements of fish so that a proper balance is achieved.

#### Areal Approaches

Several methods of recommending streamflows under current use or consideration are to varying degrees areal approaches. Included among them are those emphasizing wetted perimeter or other aspects such as surface area and food producing or shelter area. Areal concepts appear basically to be the products of the idea that more water provides habitat for more fish or fish food organisms. As noted, reasonably good correlations between stream area and fish numbers have been demonstrated, lending some credence to such approaches. Contributing to this are the relative ease of area determinations and the nature of area-discharge curves which typically show convenient breaking points beyond which area increases are small.

Several authors have questioned the value of areal approaches in assessing the carrying capacity of streams. Delisle and Eliason

(1961) stated that measurements of physical factors such as wetted area and wetted perimeter had little meaning unless they were directly related to the basic needs of fish. Several authors have found that water depth and velocity are more directly proportional to discharge than is stream area. Hill and Burkhard (1967) suggested that these habitat characteristics might be so reduced as to critically affect trout stream production without appreciable change in surface area or appearance. Hunt (1969), after examining the results of a detailed study of brook trout production in a Wisconsin stream, also questioned the validity of assessing carrying capacity of streams in terms of their surface areas. He felt that surface area was not an important determinant of carrying capacity, and that some other expression might be more realistic. Other studies have also shown that living space alone does not determine carrying capacity of stream channels (Mason and Chapman, 1965).

A review of ecological aspects of fish life in streams soon convinces one that regulation of production is not dependent on any single environmental factor, but on a complex network of factors. Strict area-production viewpoints fail to incorporate the variety of environmental criteria that are of considerable importance in influencing fish numbers. Such approaches might indicate to a degree the quantity of habitat present, but would provide no measure of its quality. For example, shelter for fish, both overhead and submerged, would seem in some instances to be influenced non-linearly by discharge level. The great importance of streambank

vegetation, undercut banks, extending roots and debris, and other stream margin characteristics to small and large fish should not be overlooked. As used by Collings, Smith and Higgins (1970), however, the breaking point on the curve of wetted perimeter probably bears some relationship to the region of streambank shelter. An additional shelter factor to consider is the increased value of substrate as cover at higher water velocities.

Another important requirement of salmonids, their food supply, relates poorly to simple areal parameters. Benthic production depends mostly on water velocity and substrate type. Invertebrate drift, frequently the major source of food of stream salmonids, is governed largely by velocity and is associated with area only in an indirect manner. Terrestrial insects falling into the stream are an important source of food for young salmonids in summer, and their numbers may be associated to some degree with surface area. However, the proximity of overhanging streamside vegetation appears to have a much greater influence on the quantity of this component of food. In addition, leaf fall and other allochthonous food materials utilized by stream insects would probably be increased as the water line approached vegetated banks.

Water quality is another factor to consider in evaluating the adequacy of areal concepts. Under reduced discharge, when a stream pulls away from shaded borders and water movement slows, temperatures may rise and oxygen levels drop dramatically. These are other aspects of habitat quality not contained in wholly spatial viewpoint.

### Potential for Microhabitat-based Methodology

Suggestions have been made that data regarding salmonid microhabitats (physical conditions immediately surrounding each animal) could be used to recommend streamflows for fish. Baldes (1968) stated that the number and diversity of microhabitats is directly proportional to the potential carrying capacity of the stream environment. Baldes and Vincent (1969) later indicated that microhabitat data could be useful in efforts to increase carrying capacity through manipulation of the environment. The Oregon Wildlife Commission collected salmonid microhabitat data in recent years with the objective of incorporating it into techniques for establishing rearing flow recommendations. More recently, Hooper (1973) suggested that existing hydraulic data be used to determine optimum flows by calculating the potential microhabitat area available at different flows. Pearson, Conover and Sams (1970) essentially utilize this approach in their "pool velocity" technique for making streamflow recommendations.

A method for determining streamflow recommendations that is based largely on the concept of fish microhabitat (that is, microhabitat as commonly interpreted and recorded) seems, as with other approaches, to be a narrow point of view. As Baldes and Vincent (1969) point out, there are several types of microhabitat used by fish for a variety of activities (i.e., resting, feeding, reproduction, etc.), all of which might be presumed to have different physical characteristics. Observations of microhabitats of young

salmonids are often limited, however, to depth and velocity measurements at locations where young fish (presumably undisturbed) were sighted in the stream. The locations commonly studied probably often represent "focal points" or conditions preferred for resting, but likely are not indicative of the range of conditions used or needed by fish for all activities. Provided this is a correct assessment, the question arises as to whether maximizing the amount of resting microhabitat would provide optimum conditions for fish.

The locations selected by fish as focal points have, in instances, been shown to be associated with nearby conditions of higher velocity and greater abundance of food drift. Achieving physical conditions that provide the greatest food drift may be a more important criterion than focal point habitat, particularly if food greatly influences habitat selection. Higher channel velocities, if desirable for food drift, might still provide ample focal point habitat since fish are able to adjust their stations vertically.

Earlier publications were noted which indicated that the distribution of juvenile salmonids frequently varied diurnally, and that nighttime habitat needs might be important in influencing density. This factor could also complicate use of present microhabitat data, which essentially consists of daytime observations only.

It is difficult to visualize how microhabitat data, as presently constituted, would be adequate of itself for use in determining flow levels. Such data might, however, be one valuable element of an advanced methodology for recommending flows, particularly if certain

species are to be emphasized in the recommendations. Microhabitat information presently consists of limited physical data not easily related to food and shelter requirements. Neither can the data be used in a spatial context. Overall, there seem to be a number of problems facing the use of such data in flow recommendations, in terms of both adequacy and implementation.

#### Usefulness of Current Methodologies - An Opinion

Based on this literature review, it seems clear that an ideal method for establishing rearing flow recommendations should take into account a broader range of environmental needs of fish than is considered in current methodologies. Such a method should attempt to mesh as many requirements as practical in such a way that an optimal balance is achieved. Of particular significance might be the elements of shelter and food supply. Present knowledge of the stream ecology of young salmonids, however, does not appear adequate for extensive development of new methodology having the degree of factual basis needed to overcome present criticisms.

The "pool velocity" and "riffle velocity-area" techniques suggested by the Fish Commission of Oregon for coho salmon are approaches based on ecological findings, and have appeal as technical ways of treating the two requirements of food supply and microhabitat. Further study or analysis of hydraulic data might reveal whether the stated pool and riffle criteria could be simultaneously achieved in stream channels, or whether adjustment would be required to provide balanced

use of both criteria. A combination would seem an improvement if both are considered to be important requirements. There is some question, however, as to the basis and reliability of the pool velocity technique. As noted, use of microhabitat (focal point) observations to calculate discharge levels may be fundamentally weak, since optimization of this criterion may not result in maximization of carrying capacity. Also, mean pool velocities in the coho study apparently ranged only up to 0.2 fps, and one wonders whether the positive relationship between velocity and fish density would extend to the recommended mean velocity of 0.7 fps.

There are elements of the approaches of other agencies that provide valuable methods for developing flow recommendations. For example, one major criterion or index of optimal fish habitat might be a measure of average velocity of water through a stream reach or in a certain habitat such as riffles or pools, while another might be a waterline adjacent to streamside cover. Use of a set of curves such as those of Collings, Smith and Higgins (1970) reproduced in Figure 6 would permit relatively simple determinations of area-velocity relations from which optimal discharge might be selected. In addition, U.S. Forest Service methodology as described by Chrostowski (1972) is one example of the combination of a variety of criteria into one habitat rating.

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