AN ABSTRACT OF THE THESIS OF

JOSEPH LEE FURNISH for the DOCTOR OF PHILOSOPHY

in ENTOMOLOGY presented on December 5, 1989

Title: FACTORS AFFECTING THE GROWTH, PRODUCTION AND DISTRIBUTION OF THE STREAM SNAIL *Juga silicula* (Gould)

Abstract approved: Redacted for Privacy

N.H. Anderson

The abundant stream snail, *Juga silicula*, was studied for four years in Oak Creek, a stream draining the eastern foothills of the Coast Range, Benton County, Oregon. A series of field and experimental investigations were conducted to examine how physical and biotic variables interact to determine the snail's growth and abundance. Temperature, population density, and food quantity and quality were of primary importance in determining snail growth rates and activity. Growth rates were depressed by cool water temperatures in the winter, by a high population density, and poor food quality. Positive growth on a variety of foods was observed, however highest growth was achieved on periphyton. Snail abundance was highest at current velocities <30 $cm \cdot sec^{-1}$, on coarse substrates and in unshaded patches. Snails of different sizes and ages were also segregated according to these physical variables.

When the biomass of *J. silicula* was reduced by a factor of six, from a normal density of 13.3 to 2.1 $g \cdot m^{-2}$, the production:biomass ratio was higher by a factor of

about five in the low-density population (0.566 vs. 0.115). Production for the population maintained at high density was 1529 $mg \cdot m^{-2} \cdot yr^{-1}$ compared to 1188 $mg \cdot m^{-2} \cdot yr^{-1}$ for the low density population. These results provide strong evidence that snail growth may be limited through intraspecific, exploitative competition for food. Dispersal was stimulated by warm water temperature, high population density and food limitation.

The knowledge gained from these studies of the seasonal abundance and distribution of *J. silicula* was also used to interpret patterns of distribution for benthic insects and to predict when snails are expected to have a significant impact on food resources and community structure. The snail exerts an impact on stream communities by exploitative competition through its ability to depress the available foods of both autochthonous and allochthonous origin. Its grazing activity results in interference competition, that mainly disturbs sedentary species. Grazing by *J. silicula* significantly reduced standing crop of chlorophyll a during 7 out of 12 months, and shredding by snails almost doubled the rate of weight loss of alder leaf packs.

These studies illustrate how a single, abundant species responds to variation in the physical environment, as well as how it exerts a pervasive influence on the availability of food resources, habitat patches and stream community structure.

FACTORS AFFECTING THE GROWTH, PRODUCTION AND DISTRIBUTION OF THE STREAM SNAIL *Juga silicula* (Gould)

by

Joseph Lee Furnish

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

Completed December 5, 1989

Commencement June 1990

APPROVED:

Redacted for Privacy

Professor of Entomology in charge of major

Redacted for Privacy

Head of Department of Entomology

Redacted for Privacy

Dean of Graduate School

Date thesis is presented December 5, 1989

ACKNOWLEDGEMENTS

I wish to express my appreciation to the following persons who each made a contribution to this thesis and my graduate education.

To Dr. N. H. Anderson, my major professor, for his assistance and guidance in conducting the research and preparation of the manuscript, and also to his contributions which broadened my education and writing skills.

To Dr. Ralph Berry, chairman, Department of Entomology, for providing the facilities and atmosphere conducive to good graduate study.

To Dr. Stanley Gregory, Dr. David McIntire, Dr. Jeffrey Miller, Dr. Victor Brookes, Dr. Christopher Bayne and Dr. Harry Phinney, all of whom provided valuable advice, information and/or review of manuscript.

To my fellow graduate students who participated in many hours of worthwhile and stimulating discussions. My special gratitude to Dr. Chuck Hawkins, Dr. Jim McIver, Dr. David Herbst and Dr. Jeff Witcosky.

To Randy Wildman and Anita Upenieks Beatty, who provided invaluable field and laboratory assistance.

To my family, especially my parents, who provided support and patience through the years that it has taken to complete this endeavor.

This research was supported by a grant from the National Science Foundation, Grant No. BSR-8306892, to Dr. N.H. Anderson and Dr. C.P. Hawkins.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

FACTORS AFFECTING THE GROWTH, PRODUCTION AND DISTRIBUTION OF THE STREAM SNAIL *Juga silicula* (Gould)

INTRODUCTION

The snail, *Juga silicula* (Gould 1847) is one of the most conspicuous benthic macroinvertebrates in lowland streams and rivers west of the Cascade Mountains. In Oregon, it commonly occurs in streams and small rivers of the Willamette Valley, foothill streams of the western Cascade Mountains and throughout the Coast Range at lower elevations. This single species often comprises over 50 percent of the standing macroinvertebrate biomass and may have a pervasive influence on stream trophic dynamics (Warren 1971, pp.316-317), yet detailed field studies of its natural history have not been done.

The snail may also exert a major influence on macroinvertebrate community structure by monopolizing periphyton resources (Hawkins and Furnish 1987). In that study, the densities of many macroinvertebrates were depressed or redistributed in response to competition with snails. It was concluded that the impact of the snail on community structure could be determined accurately only when more information was available on its natural history, habitat preferences and geographic distribution.

To examine the capacity of *Juga silicula* to influence

community-level processes, the present study was designed to examine and describe: 1) microhabitat distribution of the snail with respect to physical factors (specifically shade, substrate particle size, and current velocity); 2) its seasonal patterns of growth, production and dispersal; and 3) its utilization of autochthonous and allochthonous food resources.

These objectives were addressed in three separate manipulative field experiments as summarized in Table 1.1. Two snail populations were maintained in a concrete diversion channel adjacent to Oak Creek (Fig. 1.1). The channel was divided longitudinally by a wooden barrier. On the high-density side the snails approximated a typical field population, whereas on the low-density side, the numbers were maintained at about 10% of field density. This experimental protocol provided a comparison of the influence of snails on the stream community at normal densities with that in a treatment stream where their influence was attenuated. The high- vs. low-density comparison also was useful for determination of density-dependent growth, production and dispersal of the snail. Details of the stocking procedure and other manipulations are given in succeeding chapters as they varied depending on the experiment conducted.

Growth and dispersal of snails were also measured in Oak Creek and Rock Creek during the summer to compare

Table 1.1. Summary of experiments and measurements made in the experimental diversion channel at Oak Creek, Benton County, Oregon, from 1982 to 1985.

EXPERIMENT NUMBER	I	II	III
SAMPLING INTERVAL	1982*	1983-1984	1984-1985
FREQUENCY	ONCE (SUMMER)	MONTHLY	TWICE (WINTER-SUMMER)
MANIPULATIONS			
SNAIL DENSITY	X	X	X
SHADE	X	X	X
SUBSTRATE	X		X
MEASUREMENTS			
SNAIL GROWTH		X	X
SNAIL PRODUCTION		X	
SNAIL DISPERSAL		X	X
COMPETITIVE EFFECTS	X	X	X
CHLOROPHYLL *a*	X	X	X
BIOMASS/CHLOR *a*		X	
LEAF PROCESSING		X	

* Results of interspecific competition between *Juga silicula* and other macroinvertebrates, and the effect of snail grazing on chlorophyll *a* standing crops have been published (Hawkins and Furnish 1987).

Figure 1.1. Schematic diagram of the experimental channel at Oak Creek, Benton County, Oregon. Snails were maintained at two population densities designated as the high-density and low-density populations. The shading is arranged as in Experiment I (August of 1982). This shading arrangement was replicated at the downstream end of the channel in Experiment I. The diagram is not to scale.

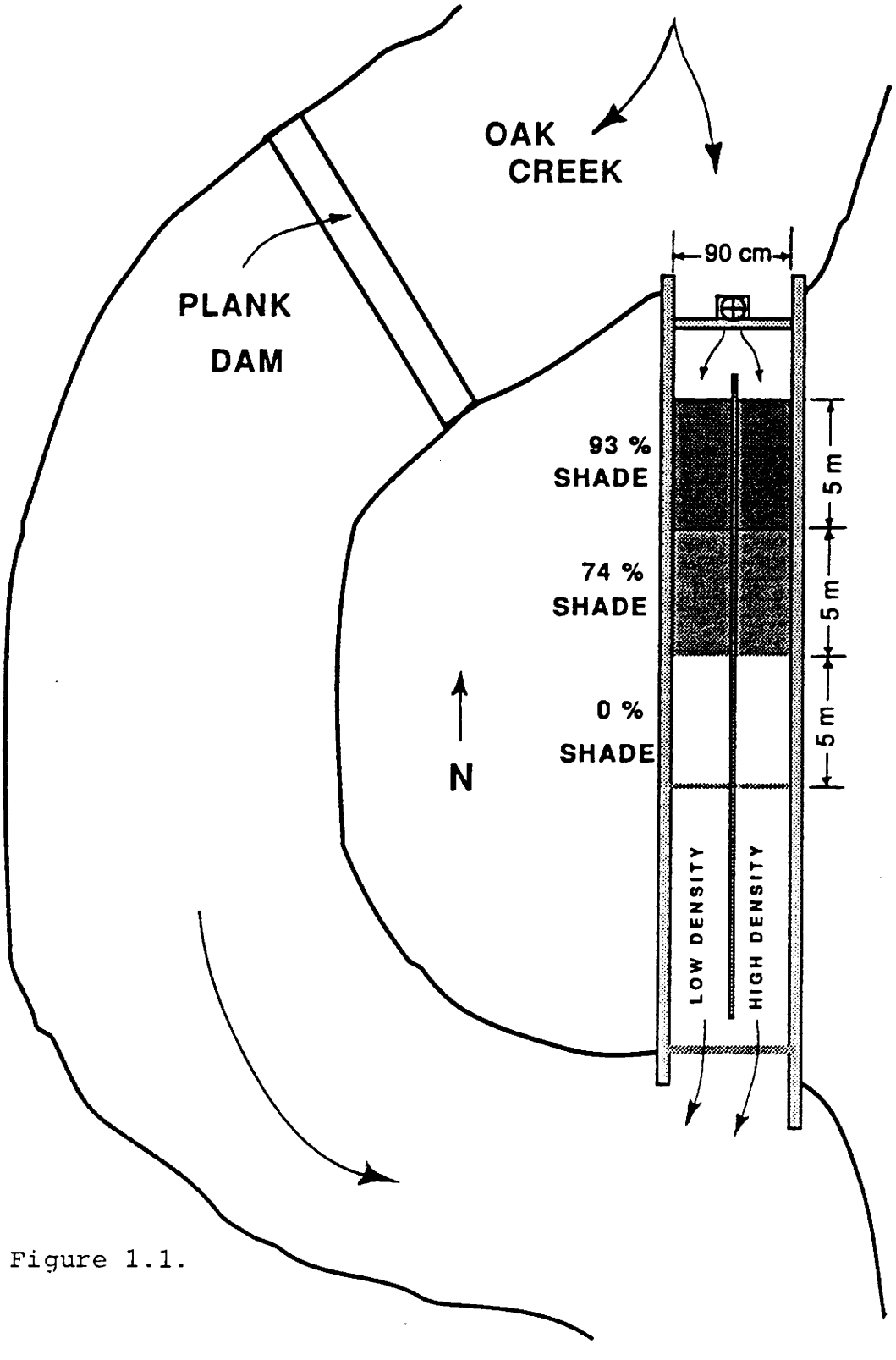

OAK
CREEK
PLANK
DAM
90 cm
93 %
SHADE
74 %
SHADE
0 %
SHADE
5 m
5 m
5 m
N
LOW DENSITY
HIGH DENSITY

Figure 1.1.

natural stream values to those of the diversion channel. Extensive benthic sampling was carried out in each stream to examine snail abundance at different current velocities and depths.

Study Areas

The main study site was at Oak Creek, a third-order stream draining the eastern foothills of the Coast Range in McDonald Forest, 10 km. northwest of Corvallis, Benton County, Oregon. Stream substrates are derived from a basalt bedrock and consist mainly of sand, gravel and cobble. Clay banks, a major feature at the Oak Creek site, contribute significantly to total suspended solids and the fine inorganic particles that accumulate in areas of slack water. Riparian vegetation consists mainly of Oregon ash (*Fraxinus latifolia* Benth.), red alder (*Alnus rubra* Bong.), bigleaf maple (*Acer macrophyllum* Pursh), Garry oak (*Quercus garryana* Dougl.) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco).

Water temperatures, measured with a maximum-minimum thermometer 2-3 times each week from July of 1983 to October of 1985, ranged from highs of about 20°C in late summer to lows of 0°C in the winter (Fig. 1.2). The mean of all water temperatures recorded for each month was highest in August at 15°C, and lowest from December through February at 5 to 7°C. Mean annual rainfall was 119 cm (Fig. 1.3). During both 1983 and 1984, rainfall peaked in November and was consistently low from July

Figure 1.2. Mean monthly temperature and temperature range from September 1983 through September 1985, measured in the diversion channel at Oak Creek, Benton County, Oregon.

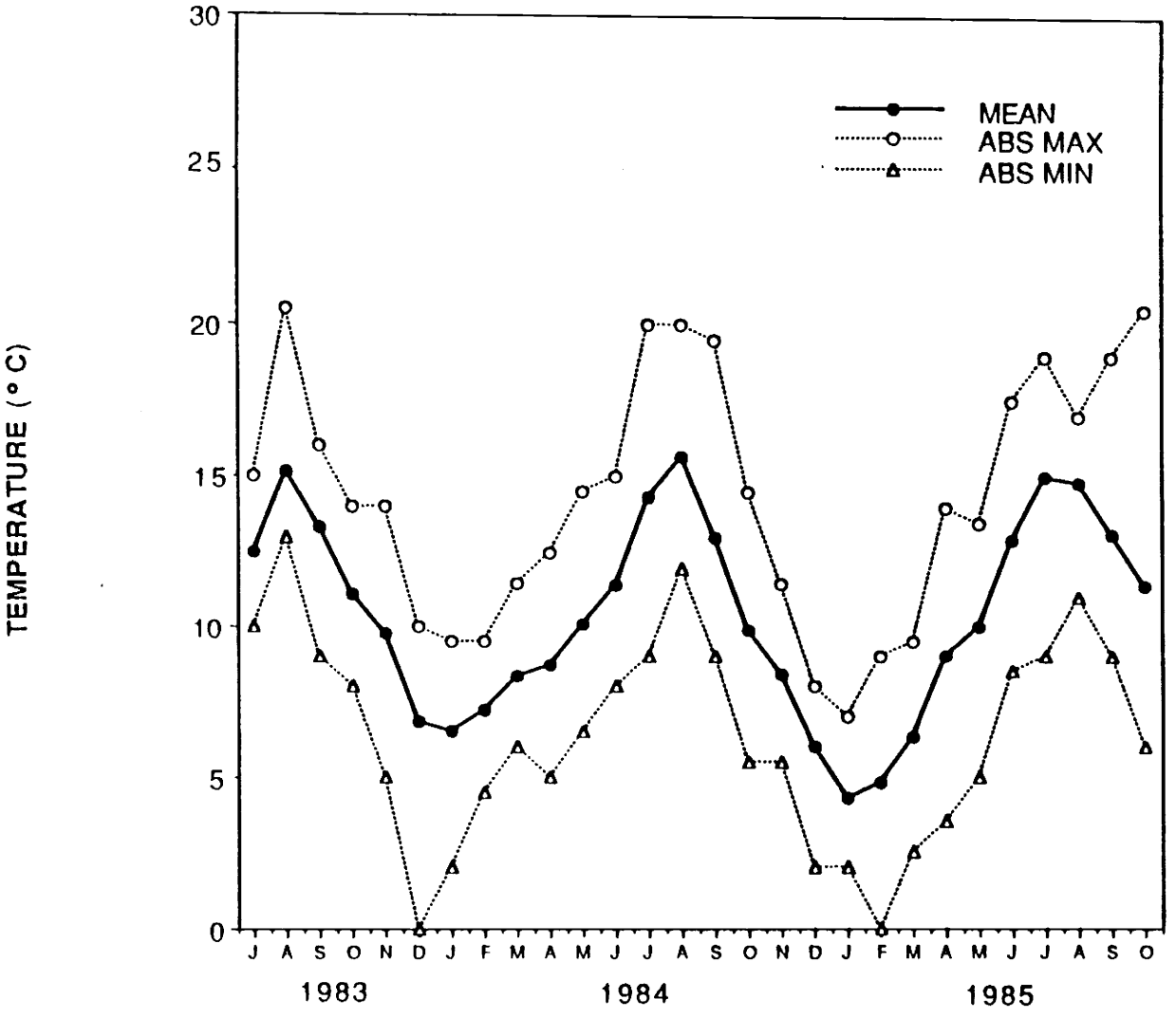

TEMPERATURE (° C)
30
25
20
15
10
5
0
MEAN
ABS MAX
ABS MIN
J A S O N D J F M A M J J A S O N D J F M A M J J A S O
1983
1984
1985
MONTH

Figure 1.2.

Figure 1.3. Total monthly rainfall from September 1983 through September 1985 measured at the diversion channel on Oak Creek, Benton County, Oregon.

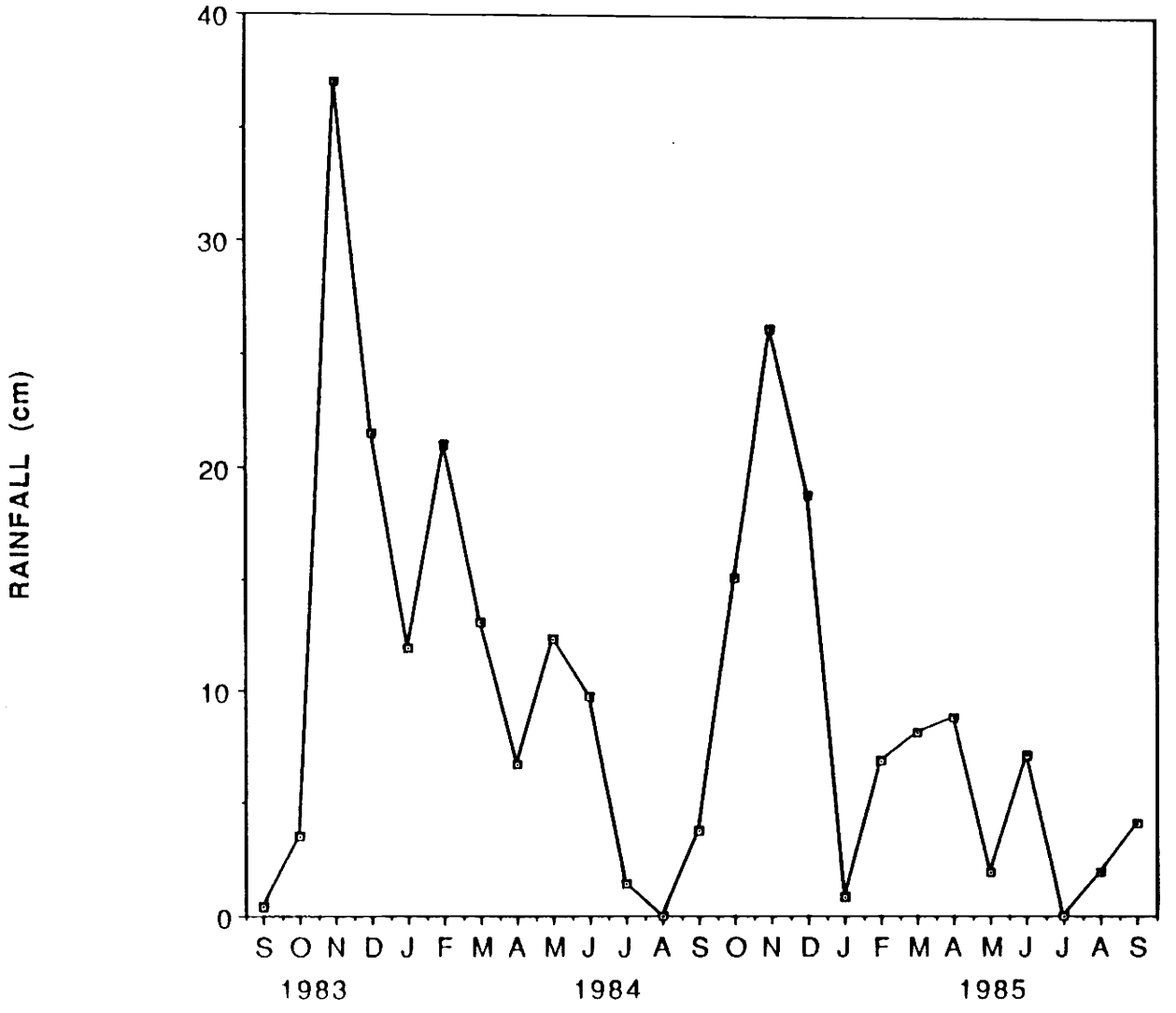

RAINFALL (cm)
40
30
20
10
0
S O N D J F M A M J J A S O N D J F M A M J J A S
1983
1984
1985
MONTH

Figure 1.3.

through September.

The study site on the North Fork of Rock Creek was above the Corvallis Watershed Reservoir on the east side of Marys Peak in the Coast Range, Benton County, Oregon. Underlying geology is a complex of sandstones, siltstones and basalt, which weather to produce cobble and gravel substrates. Riparian vegetation is mainly Douglas-fir, red alder, vine maple (*Acer circinatum*), and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.). Physical and chemical data for Oak Creek and Rock Creek are compared with data from the experimental channel in Table 1.2.

Systematics and Recent Distribution of the Family Pleuroceridae

Juga silicula is an operculate, prosobranch snail which belongs to the Family Pleuroceridae. Species in this family are characterized by dioecious reproduction, absence of a verge or penis in males, presence of an egg-laying sinus on the right side of the foot in females, and a smooth mantle edge (Burch 1982). Pleurocerids generally prefer streams with stony, silt-free substrate, moderate current velocities and depths, and high alkalinity (Dazo 1965, Houp 1970, Harman 1972, Kreiger and Burbank 1976, Ross and Ultsch 1980).

Pleurocerid snails occur in North, Central and South America, as well as in Asia and Africa (Burch 1982), but it is in America north of Mexico where they are most diverse and abundant. Burch (1982) lists 15 families and

Table 1.2. Physical and chemical characteristics of the study sites at Oak Creek and Rock Creek, Benton County, Oregon. Unless otherwise indicated, the measurements were made during this study from 1983 to 1985. When available, the range is given in parentheses.

VARIABLE	OAK CREEK	OAK CREEK DIVERSION CHANNEL	ROCK CREEK
ELEVATION (meters)	154	150	205
MEAN TEMPERATURE (and RANGE) (^{o}C)	10 (0-20)	10 (0-20)	6 (4 -12)[b]
ANNUAL RAINFALL (cm)	119	119	--
MEAN WIDTH (meters)	2.1 (0.5-2.9)[a]	0.9	2.7[c]
MEAN CURRENT VELOCITY ($cm \cdot sec^{-1}$)	40 (9-64)[a]	15 (5-30)	22[c]
MEAN DISCHARGE ($m^3 \cdot sec^{-1}$)	0.5 (.01-1.5)[a]	0.03	0.1[c]
NITRATE ($mg \cdot l^{-1}$)	--	--	0.5[b]
CALCIUM ($mg \cdot l^{-1}$)	--	--	10[b]
HARDNESS ($mg \cdot l^{-1}$ as $CaCO_3$)	(17-34)[a]	--	37 (25-39)[b]
pH	7.2[a]	--	7.3[b]

a. Speir (1975).
b. Water Quality Laboratory, City of Corvallis, 1983.
c. Hiram Li, Oregon State University, unpublished data, 1983.

499 species of freshwater gastropods in North America, of which 153 species or 30% are pleurocerids. Eighty-three species belong to the eastern genus *Elimia*, while in the west *Juga* is represented by 11 species (Henderson 1935, Taylor 1981, Burch 1982).

In North America north of Mexico, pleurocerid species are widely distributed throughout the Mississippi and Ohio River Valleys, the Appalachian Mountains and Piedmont Plateau of the Atlantic and Gulf states, the Ozark Plateau, and tributaries of the Great Lakes and St. Lawrence River. They occur as far south as the Brazos and Guadeloupe Rivers in Texas (Goodrich 1942a) and the Hillsborough River near Tampa, Florida (Burch 1982).

In the Pacific Northwest and northern Great Basin the family is represented only by the genus *Juga* (formerly *Goniobasis* and *Oxytrema*) (Taylor 1981, Burch 1982), which has been further divided into four subgenera: *Juga*, *Calibasis*, *Oreobasis* and *Idabasis* (Taylor 1966). The subgenus *Juga* is represented by three species (*silicula*, *plicifera* and *hemphilli*) and is most common and widely distributed west of the Cascade Mountains. *Juga silicula* occurs as far north as the Quinault River on the Olympic Peninsula and south to the lower Trinity River in Humboldt County, California. The subgenus extends east of the Cascades in tributaries of the Columbia River to the mouth of the Deschutes River (Fig. 1.4). Generally *J. silicula* is confined to streams and small rivers, while *J.*

plicifera occupies large rivers (Burch 1982). *Juga hemphilli* is known only from its type locality "near Portland" (Henderson 1935) and the Long Tom River, a tributary of the Willamette River (D.W. Taylor, personal communication).

Although Henderson (1929) and Burch (1982) consider *J. silicula* and *J. plicifera* to be distinct species, Clarke (1981) considers them to be synonymous. Difficulties that arise in making accurate specific determinations are largely the result of the extensive variability in shell morphology commonly exemplified by conspecifics of this family. This variability has been exhaustively studied for only a few species of pleurocerids (Adams 1915, Baily et al. 1933), but causative agents remain obscure. Henderson (1929) found no evidence of intergradation or co-occurrence between the two species. He described *silicula* as having longitudinal ribs confined to the apical third in adult shells (in *plicifera*, ribbing extends to the shell aperture) and a more slender shell than *plicifera*.

Erosion of the shell apex is a common phenomenon that causes variability in shell morphology. It is the result of physical abrasion by particles carried in the water (Baily et al. 1933, Gore 1983) and chemical dissolution of the calcium carbonate matrix. A red alga, possibly the haploid form of *Batracospermum* or the diploid form of *Audouinella*, grows on the apical spires of the shell and

Figure 1.4. Map showing the distribution of *Juga silicula* in the Pacific Northwest. Each point represents a collection locality established during this study or taken from museum records (see Appendix B).

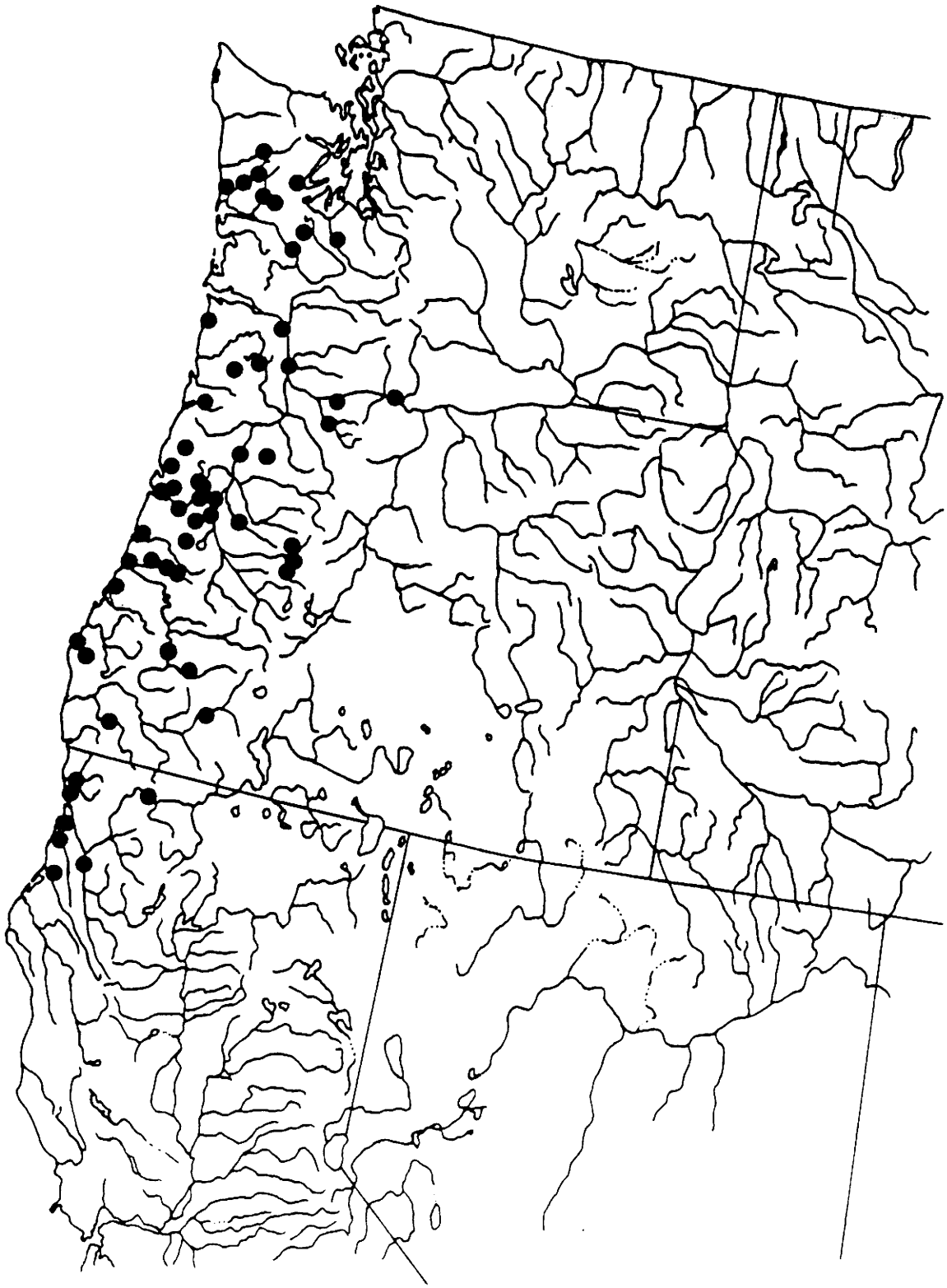


Figure 1.4.

produces carbonic acid as a by-product of respiration, which dissolves the shell (Harry Phinney, personal communication). As a result of erosion, many adult shells do not retain the first three to four spires, making it nearly impossible to distinguish some species.

The remaining three subgenera are found in Oregon, Idaho, Nevada and California. *Calibasis* occurs in the Klamath and Pit River drainages, the lower Sacramento River, and the Honey Lake basin, all in northern California (Taylor 1981,1985b). The subgenus *Oreobasis* occurs in the lower Columbia, Deschutes and Owyhee Rivers, headwater streams and springs of northern California and southern Oregon, and a few artesian springs in northeastern California and northwestern Nevada (Goodrich 1942b, 1944, Taylor 1981, Burch 1982). *Idabasis crysopylica* is known only as a fossil from the Petaluma Formation of the Pliocene Epoch, 5 million years before present (mybp), with localities in the Central Valley of California and southwest Idaho (Taylor 1966).

Historical Biogeography of the Family Pleuroceridae

Pleurocerids first appear in the fossil record in the Laramie Formation (Upper Cretaceous, 65 mybp) with localities in Colorado, Utah, Wyoming, Montana, Alberta and Saskatchewan. This period marks the beginning of the Laramide Orogeny in western North America in which the Basin and Range and Colorado Plateau were broadly uplifted and deformed (Minckley et al. 1986). During the late-

Cretaceous the North American continent, which had been divided by the Midcontinental Seaway during the mid-Cretaceous (Hocutt and Wiley 1986), began to dry up and freshen as the Laramide Orogeny proceeded until the end of the Paleocene epoch (58 mybp). Under these conditions, huge lakes (e.g. Green River Lakes) and drainage patterns began to form providing ideal habitat for molluscs and resulting in an impressive diversification. Of the 199 aquatic species recognized by White (1883) in his classic monograph on non-marine fossil molluscs from the Devonian to recent, 131 (65%) of the total, and 14 out of 19 pleurocerid species (73%), were unique to the Laramie formation.

Pleurocerid fossil records exist from the Upper Cretaceous to the Pliocene and Pleistocene epochs indicating that the family was widely distributed within the extensive lacustrine habitats that have since disappeared from the Great Basin and Great Plains (Dazo 1965, Taylor 1966,1985a,1985b). White (1883) presented a compelling argument for an origin of the Pleuroceridae in western lakes and a subsequent eastward migration through ancient river channels to assume their present distribution. The distribution of fossil and recent molluscs, and fish in the west reveal two faunal connections: 1) between the Snake River Plain south-westward to the Pacific Slope in the region of the Sacramento and Klamath Rivers, and 2) within a "fish-hook

pattern" extending from the Snake River Plain along the north and western margins of the Great Basin as far south as the Mojave Desert (Taylor 1966,1985b, Taylor and Smith 1981, Minckley et al. 1986). This distribution pattern suggests a connection between the Snake River and Pit River in northwestern California, which is believed to have existed until the Pliocene (Minckley 1986) and may well have served as a dispersal route from southwestern Idaho to the Klamath Mountains and the Sacramento River.

A single fossil of *J. silicula* has been recovered from the Clarkia fossil site in northern Idaho which suggests that it was more widely distributed in the west during the Miocene (Taylor 1985a). Analysis of a variety of plant and animal fossils from this site suggest a warm-temperate and humid climate with a "diversified mixed mesophytic forest similar to those now occupying the hill-and-valley topography of the southern foothills of the Appalachian Mountains, admixed with taxa now restricted to forests of similar climatic/topographic setting in eastern Asia" (Smiley 1985, 416).

In addition to Pleuroceridae, the families Viviparidae and Unionidae are also abundant as fossils in the Laramie formation (Adams 1915) and are presently widespread in the eastern United States (Burch 1982). Unlike the Pleuroceridae, the family Viviparidae does not presently occur west of the Rocky Mountains and the family Unionidae is poorly represented by two thin-shelled

genera: *Anodonta* and *Gonidea*. Henderson (1929) stated that this region is the largest area in the world destitute of heavy-shelled Unionidae.

An alternative, less widely-accepted theory on the origin of pleurocerids states that they originated in the southeastern United States and spread westward. Adams (1915) cites two factors which support this view: 1) the impressive abundance of pleurocerid species in the southeast which suggests vicariant endemism (i.e. geographic isolation of populations via headward erosion of streams) and 2) their confinement to fluvial habitats in geologically stable channels that are not suitable for fossil preservation because of prolonged erosion and repeated base-leveling. This latter condition would explain the absence of fossils from the eastern United States, where favorable habitat for pleurocerids has existed since the late Cretaceous.

The above discussion of pleurocerid paleobiogeography offers two explanations for the strikingly disjunct distribution of this family. These events emphasize an adaptability to both lacustrine and riverine habitats, paralleled by the present distribution of *J. silicula*. This species is mainly a denizen of clear, fast-flowing, forested streams and rivers characterized by clean, coarse substrates. However, its distribution extends to littoral zones in Coast Range and coastal lakes (e.g. Tahkenich Lake and Carter Lake), headwater trickles, and low

gradient coastal rivers in which fine sediments predominate (e.g. Alsea River at Tidewater, Humptulips River).

Biology of *Juga silicula*

Juga silicula is one of the most abundant macroinvertebrates in lowland streams and rivers west of the Cascade Mountains, and in many streams it may comprise a major portion of the standing biomass. For example, Diamond (1982) observed densities as high as 2350 snails per m^2 in a controlled-flow section of Berry Creek, a small stream in the Willamette Valley, Benton County, Oregon. In some streams this snail may reach a standing crop of 37 $g \cdot m^{-2}$ total body ash-free dry mass and comprise greater than 90% of the total macroinvertebrate biomass (Hawkins and Furnish 1987).

The ability of *J. silicula* to occupy a variety of habitats from small headwater streams to large rivers and lakes, as well as its generalist and opportunistic feeding habits best account for its abundance. Although it is considered to be a grazer that feeds primarily on periphyton, it may concentrate on other food sources when they are available, such as leaf detritus in the fall and carrion when it is encountered.

Snails generally live for 5-7 years and reach reproductive maturity after 3 years. The females produce 1 (or rarely 2) gelatinous egg masses per year containing an average of 150 embryos (Diamond 1977, Hawkins and

Furnish 1987). Mating is believed to occur during the fall, and egg laying commences the following spring. Eggs are generally attached to the undersides of cobble-sized stones in riffles. They are found from late March to August, with a peak in late June. Hatching occurs about a month after oviposition. Baldwin et al. (1967) reported that snails kept in the laboratory at 17-18°C laid egg masses from December 15 to February 1, and from March 1 to August. They also reported that eggs hatched approximately 10 days after oviposition, and that snails infected with mature cercariae of *Nanophyetus salmincola* were also able to produce viable egg masses.

Winter flooding appears to be the major cause of mortality, although parasitism and predation may also be significant. Diamond (1982) found that large numbers of snails died after floods deposited them on stream banks and that flood mortality rates were inversely related to stream size.

Virtually every population of snails is infected with trematode parasites (Law 1976). Based on dissections, Diamond (1977) reported that the incidence of parasitism varied from a low of 0% for a first-order tributary of Oak Creek to 92% in the Siletz River, which is a sixth-order river; in Oak Creek near the diversion channel, 75% of the population was found to be infected. The incidence of parasitism within a population increases with individual size and stream order (Gebhardt 1966, Diamond 1977).

Snails serve as intermediate hosts for several trematode species, and the most common of these locally is *Nanophyetus salmincola* (Chapin), which has recently been shown to infect humans in the Pacific Northwest (Eastburn et al. 1987). Virtually nothing is known about the effect of parasitic infection on growth rates of *J. silicula*. Trematode parasites generally attack the digestive gland in snails and infection often leads to castration and gigantism, but the mechanism of this alteration in growth is still unclear (Wright 1971, Bayne and Loker 1987).

Principal vertebrate predators of *J. silicula* include Pacific giant salamanders (*Dicamptodon ensatus*) and reticulate sculpins (*Cottus perplexus*). Warren et al. (1960) reported that *J. silicula* comprised 68% of the number of prey ingested by *D. ensatus*, and 41% ingested by *C. perplexus* in Berry Creek. Predation on snails was size-specific; small snails (up to 3 mm shell length) were eaten most often. According to R. Wildman (personal communication), in late August, 1989, six 10-20 cm-long *D. ensatus* captured in Lookout Creek in the H.J. Andrews Forest near Blue River, Lane County, Oregon had all ingested *J. silicula*. Most salamanders had from 7-10 snails in their guts, with a maximum of 15, and a maximum size of 15 mm shell length. Larger salamanders appeared to have ingested larger snails. Cutthroat trout (*Salmo clarki*) rarely ingest snails (Warren et al. 1964).

The remaining chapters focus on the following aspects

of the biology of *J. silicula*: (II) physical factors affecting microhabitat distribution, (III) density-dependent growth, production and dispersal, (IV) contribution to the processing of leaf litter, and (V) a synthesis describing the role of *J. silicula* in stream ecosystems.

CHAPTER II

PHYSICAL FACTORS AFFECTING THE MICRODISTRIBUTION OF THE STREAM SNAIL, *Juga silicula*: THE IMPORTANCE OF SHADE, SUBSTRATE AND CURRENT VELOCITY

Abstract

Factors affecting the abundance and distribution of *J. silicula* were determined in a stream diversion channel by manipulating shade and substrate particle size. Microdistribution of individuals was size-dependent; large individuals were most abundant in unshaded areas with coarse (5-10 cm) substrates, and small individuals were present at highest densities in shaded areas with fine (1-2 cm) substrates. During the winter, no preference for any shade treatment was observed. However, large individuals preferred coarse substrates during both summer and winter. Abundance in field populations was inversely related to current velocity. Neither snail number nor biomass were significantly correlated with water depth over a range from 1-60 cm.

Food availability, measured as standing crop of chlorophyll a and detritus, was not correlated with total snail biomass. However, the mean size of individuals in a substrate patch decreased with substrate particle size. Smaller snails were most abundant on fine substrates (1-2 cm) where standing crop of chlorophyll a was highest. These findings suggest that finer substrates, where periphyton was most abundant, were inaccessible to larger individuals because the interstitial spaces were too small for them to enter and graze.

Some aquatic insects shifted their distribution when snails were removed. Taxa for which highest density

shifted from shaded to unshaded areas when snail density was reduced were: the mayflies, *Cinygmula* and *Paraleptophlebia*; the chironomid midges *Micropsectra* and *Stempellinella*; and the stonefly *Zapada/Malenka*. These five taxa exhibited microhabitat shifts only during the summer when snails were mainly concentrated in unshaded patches. During the winter when snails showed no preference for any shade level, the densities of all five taxa were uniformly depressed in the stream with higher snail density regardless of light intensity. The results suggest that the relative abundance of some macroinvertebrates across shade and substrate habitat patches is determined by competitive displacement, the intensity of which varies according to the seasonal habitat preferences of snails.

Introduction

Although many studies have shown responses of stream macroinvertebrates to specific physical variables such as light (Townes 1981, Hawkins et al. 1983, Behmer and Hawkins 1986), substrate (Minshall 1984) and current velocity (Bournaud 1963, Statzner and Higler 1986), few have described responses to these variables as a function of season, and size or age (but see Gee 1982, Pringle 1982, Adams et al. 1987). The capacity of a species to occupy a specific microhabitat will change with body size but this factor is usually not taken into consideration. For a relatively long-lived animal that takes several years to complete its life cycle, microhabitat preferences and restraints may be especially variable.

The stream snail, *Juga silicula* (Gould) is an abundant and conspicuous, long-lived macroinvertebrate in the Pacific Northwest. In an experimental stream study, Hawkins and Furnish (1987) found that *J. silicula* preferred unshaded habitats and substrates of intermediate (2-5 cm in diameter) particle sizes, but they did not examine the size-specific or seasonal aspects of this response. The goal of this study was to describe microhabitat preferences of *J. silicula*, emphasizing changes with age, size and season. Specifically, the snail's responses to light availability, particle size of substrate, and current velocity were examined in a series of field studies. Knowledge of these responses was then

used to interpret variable competitive effects by the snail on co-occurring macroinvertebrates.

Methods

The study was conducted in two streams located in the eastern foothills of the Coast Range of Oregon. The main study site was on Oak Creek about 10 km NW of Corvallis, Benton County, Oregon. Samples were taken in the natural stream and in a concrete diversion channel (see below) with a Hess sampler (0.02 m^2, mesh size 250 micrometers). A second series of samples was collected from Rock Creek within the Municipal Watershed for the City of Corvallis. Physical characteristics of the streams near the study sites are given in Chapter I.

Experimental Stream Studies

Manipulative experiments were conducted in an experimental channel that has been described by Hawkins and Furnish (1987). Briefly, a 90-cm-wide, concrete-walled diversion channel with a gradient of 2% was divided lengthwise to create two streams. The 30-cm-high board dividing the channel was braced by 10-cm-high cross dividers which created a series of "stairstep" sections. The cross dividers were pushed into the substrate surface and appeared to present no significant barrier to movement either over or under them. Each channel was generally maintained at a discharge of 0.03 $m^3 \cdot sec^{-1}$ and a mean current velocity of 15 $cm \cdot sec^{-1}$ measured with the fluorescent dye, Rhodamine B (Hubbard et al. 1982). One

stream was seeded with snails from Oak Creek, and the other was maintained at a low density by removing snail immigrants every 3-4 days.

Three studies were conducted in the diversion channel to examine snail distribution with respect to shade and/or substrate. The experimental design utilized in the first study has been described by Hawkins and Furnish (1987). Plastic trays (0.05 per m^2) were filled with uniform mineral substrates of 1-, 2-, 5- or 10-cm diameter and placed randomly under shade treatments of 0, 74 and 93% light reduction. Treatments were arranged with the 93% shade treatment upstream and the 0% treatment downstream in order to minimize export of periphyton from open to shaded areas, which could have confounded the results. Ten trays (2 replicates per substrate treatment except for the 5 cm size which had 4 replicates) were placed under each shade treatment. The trays were placed immediately adjacent to the channel divider, leaving a 20-cm gap between the edge of the tray and the outside walls. This gap was filled with 5-cm gravel, flush with the top of the trays. One side of the channel was seeded with snails to create a density typical of Oak Creek during the first week in April. The other side was not stocked and was maintained at a low density. Immigration into the low-density channel from the high-density population was high so snails had to be removed twice each week to maintain the low-density population.

On August 5, after 18 weeks, the trays were removed from the channel and the snails collected from each tray were counted. Shell lengths of over 2000 individuals were measured to the nearest 0.1 mm. Total biomass for each sample was determined by converting shell length (cm) to total body ash-free dry mass (mg AFDW) by the following equation:

$$\text{Total Body AFDW} = 8.13\ (\text{Shell Length})^{3.10}, \qquad (4.1)$$

where n=30 and r^2=0.96. Total body AFDW includes the organic component of the shell, as well as body tissues.

In experiment II, monthly samples were taken to assess the seasonal response of snails to shade. Substrate size throughout the channel was 5 cm. Shade was manipulated at increments of 0, 74, 93 and 100%. Percent shading was measured by placing a light meter (LI1776 Solar Monitor; Licor, Inc.) directly underneath the screen. The screen shading was nailed to wooden frames that were suspended approximately 80 cm over the water. Even though no light was detected passing through the canvas-covered frames in the 100% shade treatment, some incident light was transmitted to the stream underneath them from adjacent shade treatments. Shading increments were arranged in random order within each of three consecutive blocks along the length of the channel.

Hess samples were taken each month from September 1983 to August 1984. Each month, 36 samples were collected (4 shade x 3 replicates x 3 blocks). Subsequent

analysis of these samples varied from month to month depending on whether replicates were processed separately or combined. All samples taken in January were processed separately. However, because of the prodigious effort and time required to process samples, the three replicates within each shade treatment were combined for September of 1983, and August of 1984, yielding 12 samples (4 shade x 3 block). For all remaining months, the 3 replicate and 3 block samples taken from each shade treatment were combined to yield 4 samples for analysis; one combined sample from each shade treatment. This procedure clearly sacrificed data on sample variability due to block and replicate position. Subsequent analysis of the samples from September 1983 revealed a block effect for both number and biomass. In August 1984 there was a block effect for snail number, but not for biomass. There was no block effect for either snail number or biomass in January.

In experiment III, two shade levels (0 and 93%) and 5 substrate sizes ranging from coarse sand to cobble (0.1, 1, 2.5, 5, 10 cm diameter) were arranged as three randomized blocks along the length of the channel in mid-August 1984. Snail density was maintained in the manner previously described. During the winter (mid-February) and summer (mid-July) of 1985, three replicate Hess samples were collected from each section and mean shell length, density and biomass of snails associated with each

treatment were calculated. Standing crop of chlorophyll a was measured during February, May and July. For substrates 0.1, 1 and 2.5 cm in diameter, approximately 30 cm^3 was removed from the surface of the substrate for analysis. Three 5-cm-diameter stones and one 10-cm-diameter cobble were utilized for those substrate sizes.

The porosity of substrates was measured by volume displacement (Pollard 1955). For the sand, a correction was made for the water held by capillary action; the sand was oven-dried and the weight lost was used to calculate the volume retained in the sand by capillary action. Volume decanted was adjusted for capillary action to calculate porosity of sand.

The standing crops of periphyton in experiments I, II and III, and detritus (>1 mm) in experiment I were determined as a measure of food availability. Periphyton was measured as standing crop of chlorophyll a in the manner described by Hawkins and Furnish (1987). The detrital fraction <1 mm in diameter was not measured because snails grew poorly on this material in the laboratory (refer to chapter III). Detritus that had accumulated in each tray was sieved to retain the fraction >1 mm, dried at 55°C, and AFDW was determined by weight loss after combustion at 550°C for 4 hours.

Shade and substrate treatment effects on snail density and biomass (transformed to log(x+1), Elliott 1977) for experiments I and III were compared by two-way

ANOVA. When the ANOVA revealed a significant treatment effect, differences between means were assessed by the Student-Newman-Keuls (SNK) multiple range test.

In experiment II it was not possible to determine the variability within treatments because samples were combined for most dates. Therefore, monthly distribution of snail biomass with respect to shade was assessed by X^2 analysis with a null hypothesis that biomass was evenly distributed over shade treatments.

Field Studies

Fifty-four Hess samples were taken in Rock Creek and Oak Creek from a variety of habitats representing a range of current velocities, substrates and depths during April and May of 1984, respectively. For each sample, current velocity was measured 5 cm above the substrate, or at mid-depth in shallower water, with the Montedoro-Whitney flow velocity meter (Model PVM-2). Substrate size distribution was measured in the field by sieving the sample through a series of screens (64-, 16-, 4-, 1- and 0.25-mm mesh) and estimating the relative volume of each inorganic substrate size class retained. Median particle size for each sample was determined by a formula given by Tolkamp (1980). Snails were counted and measured, and biomass was calculated by the methods described previously.

The influence of physical factors on density and biomass of snails was assessed by application of the Kruskal-Wallis rank sum test. The influence of current

velocity, median particle size and depth was assessed by multiple regression. Each sample was assigned to one of six habitat categories: riffle, pool, compacted clay bank, back water, boulder cascade or bedrock.

Results

Experimental Channel

Responses of snails in both high- and low-density populations were similar, but data are presented only from the high-density population because numbers in the low-density population were so small that meaningful statistical comparisons could not be made.

In experiment I, shade treatment significantly affected the mean size, density and biomass of snails (Table 2.1). Mean size decreased as shading increased (Table 2.2). Largest individuals (i.e. mean shell length >10 mm) were found on the two coarsest substrates (i.e. 5 and 10 cm diameter). On finer substrates (1 and 2 cm diameter), mean shell length was <8 mm. In all cases, highest densities were found in unshaded sections and lowest densities were found in 74% shade (Fig. 2.1). The intermediate density in the 93% shade treatments is partly attributable to a positive rheotaxis behavior, which concentrated snails at the upstream end of the channel where the high shade treatment was located (see Chapter III).

A nearly significant difference ($P<0.10$) in biomass was observed with respect to substrate particle size in

Table 2.1. Summary of two-way ANOVA results showing shade and substrate treatment effects on mean snail size (shell length), snail number and biomass, detritus accumulation and chlorophyll a standing crops. Data are from experiments conducted in the artificial channel at Oak Creek, Benton County, Oregon. Detritus was not measured in Experiment III. NS= Not significant, (*)=p<0.10 , *=P<0.05, **=P<0.01, ***=P<0.001.

TREATMENT	SIZE	DENSITY	BIOMASS	DETRITUS	CHLOROPHYLL a
EXPERIMENT I					
SHADE	***	**	**	**	NS
SUBSTRATE	**	NS	(*)	***	***
EXPERIMENT III					
FEBRUARY					
SHADE	NS	**	***	--	**
SUBSTRATE	NS	NS	NS	--	***
JULY					
SHADE	NS	NS	**	--	***
SUBSTRATE	NS	NS	(*)	--	***

Table 2.2. Mean size of snails and amount of detritus >1 mm associated with shade and substrate treatments in experiments I and III in the diversion channel at Oak Creek, Benton County, Oregon. Treatments with different letters are statistically different by Student-Newman-Keuls multiple range tests. (Detritus was not measured in Experiment III).

			EXPERIMENT I				EXPERIMENT III			
			DETRITUS > 1 mm		SHELL LENGTH ($\bar{X}$)		SHELL LENGTH ($\bar{X}$)			
TREATMENT		POROSITY					February		July	
		%*	($g \cdot m^{-2}$)	SIG.	(mm)	SIG.	(mm)	SIG.	(mm)	SIG.
SHADE (%)	0		24.3	a	10.11	a	13.6	NS	6.76	NS
LEVEL	74		22.5	a	9.59	ab	---		---	
	93		46.1	b	7.83	b	14.1		4.41	
SUBSTRATE	0.1	37.6	---		---		14.5	NS	5.37	NS
PARTICLE	1	41.2	6.5	a	7.84	a	14.3		3.17	
SIZE	2.5	41.2	22.3	b	7.27	a	14.2		5.92	
(cm)	5	41.5	45.8	c	10.19	b	12.3		4.07	
	10	45.1	43.2	bc	10.66	b	13.9		9.39	

* % refers to portion of total volume that is interstitial space.

Figure 2.1. Densities of *Juga silicula* within different shade and substrate treatments on August 5, 1982 in the experimental channel at Oak Creek, Benton County, Oregon (Experiment I). Values are means ± 1 SE.

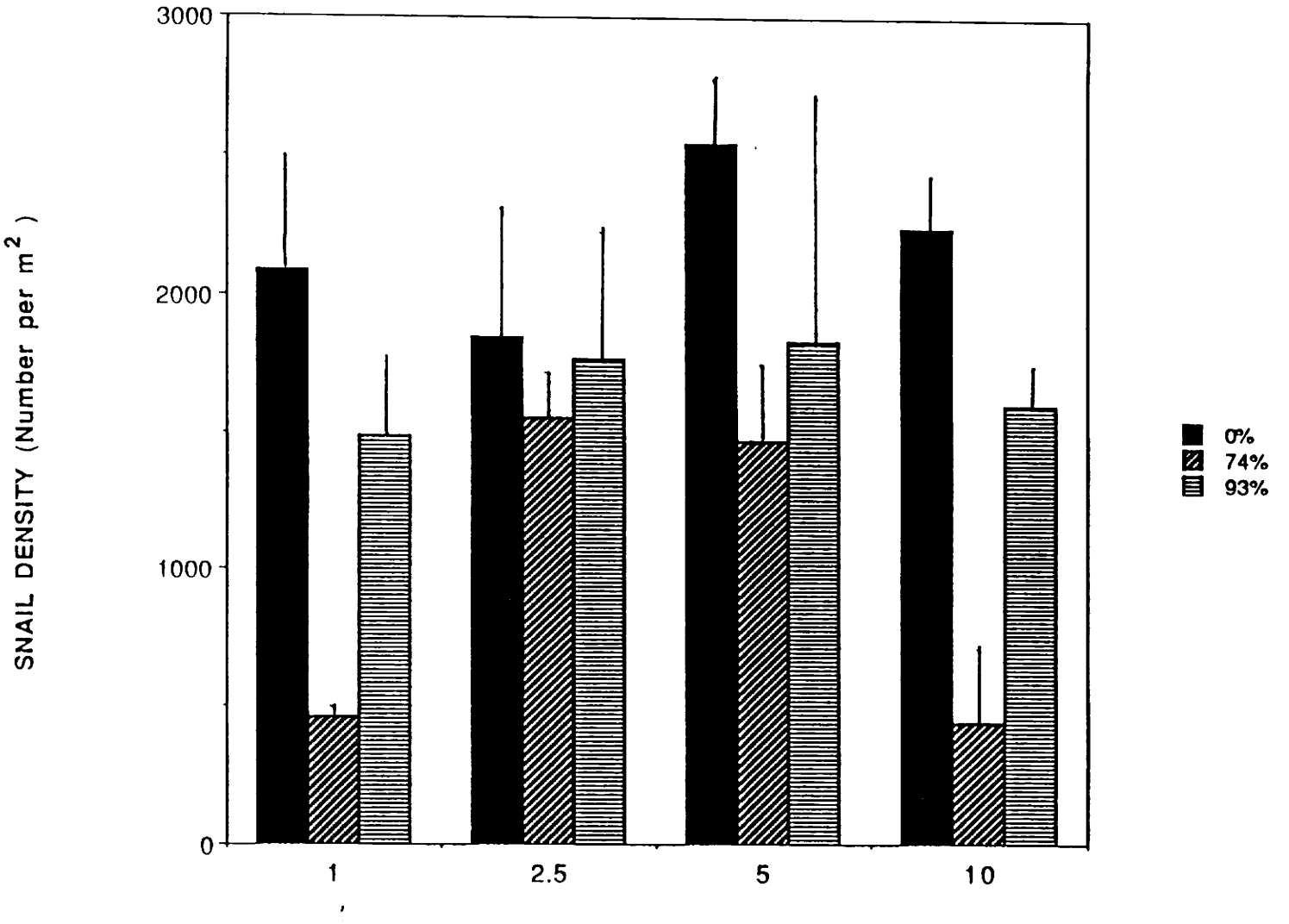

3000
2000
1000
0
SNAIL DENSITY (Number per m^2)
1
2.5
5
10
SUBSTRATE PARTICLE SIZE (cm)
0%
74%
93%

Figure 2.1.

Experiment I, and during July in experiment III (Table 2.1). Highest biomass of snails was consistently associated with unshaded and coarse substrates (5 and 10 cm, Fig. 2.2). Mean biomass varied from 46 $g \cdot m^{-2}$ on unshaded cobble and 39 $g \cdot m^{-2}$ on unshaded 5-cm gravel, to 11 $g \cdot m^{-2}$ or less on shaded gravels of small diameter.

Snail density and biomass was usually highest in unshaded sections. During nine months of experiment II density was highest in the unshaded sections (Fig. 2.3). Snail density was highest in shaded sections during September (74% shade), October (93%) and December (100%). Biomass was greatest in unshaded sections during all months except January and February (Fig. 2.4). Intermediate biomass values were observed for intermediate shading levels in September, October and from April to July.

In both summer and winter of 1985 (experiment III), snail biomass was greatest on coarse substrates, but the distribution of biomass with respect to shade differed between these two seasons. In the summer, the preference for cobble over other substrate sizes was still evident (Fig. 2.5a), however snails also showed a clear and consistent preference for unshaded conditions within each substrate class. During the winter, snails were most abundant on unshaded cobble, followed by shaded cobble (Fig. 2.5b). Snails occurred with equal frequency on the remaining available combinations of shade and substrate.

Number and biomass of the 0+ age class (shell length

Figure 2.2 Biomass of *Juga silicula* within different shade and substrate treatments on August 5, 1982 in the artificial channel at Oak Creek, Benton County, Oregon (Experiment I). Values are means ± 1 SE.

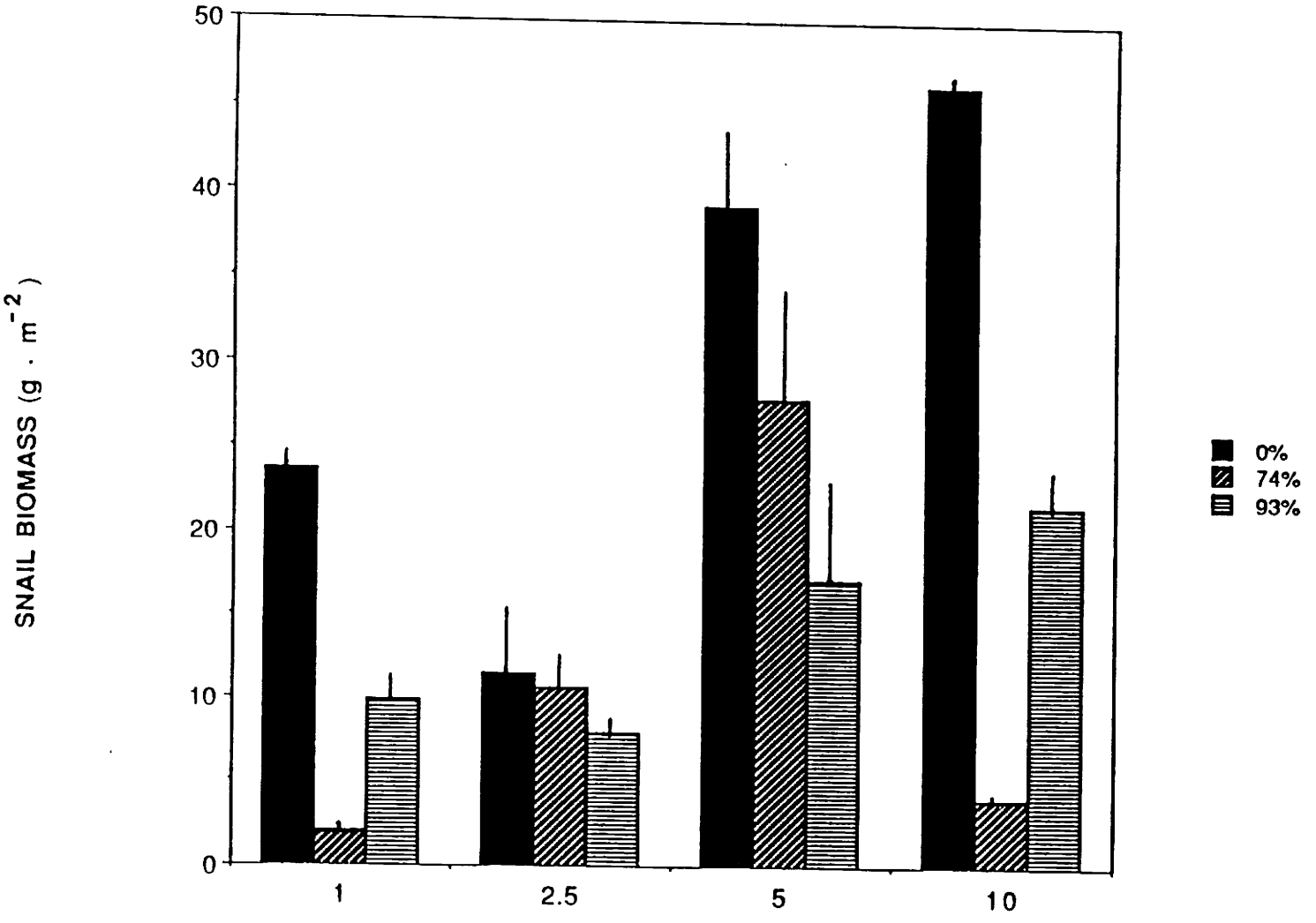

SNAIL BIOMASS (g · m^{-2})
50
40
30
20
10
0
1
2.5
5
10
SUBSTRATE PARTICLE SIZE (cm)
0%
74%
93%

Figure 2.2.

Figure 2.3 Monthly densities of *Juga silicula* with respect to shade treatments from mid-September 1983 to mid-August 1984 in the diversion channel at Oak Creek, Benton County, Oregon (Experiment II). Substrate size was not manipulated.

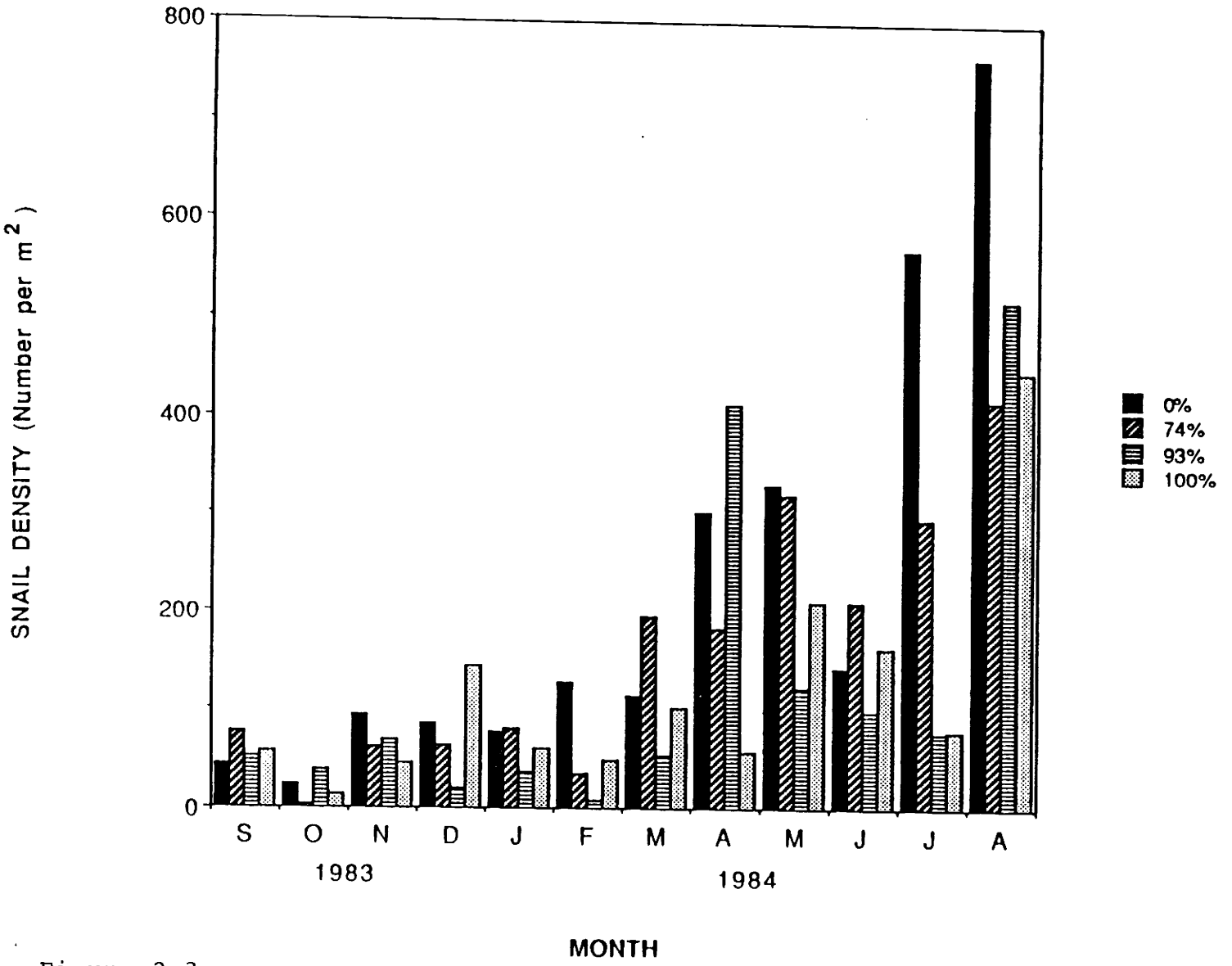

800
600
400
200
0
SNAIL DENSITY (Number per m 2)
S
O
N
D
J
F
M
A
M
J
J
A
1983
1984
MONTH
0%
74%
93%
100%

Figure 2.3.

Figure 2.4. Monthly biomass of *Juga silicula* with respect to shade treatments from mid-September 1983 to August 1984 in the diversion channel at Oak Creek, Benton County, Oregon (Experiment II). Substrate size was not manipulated.

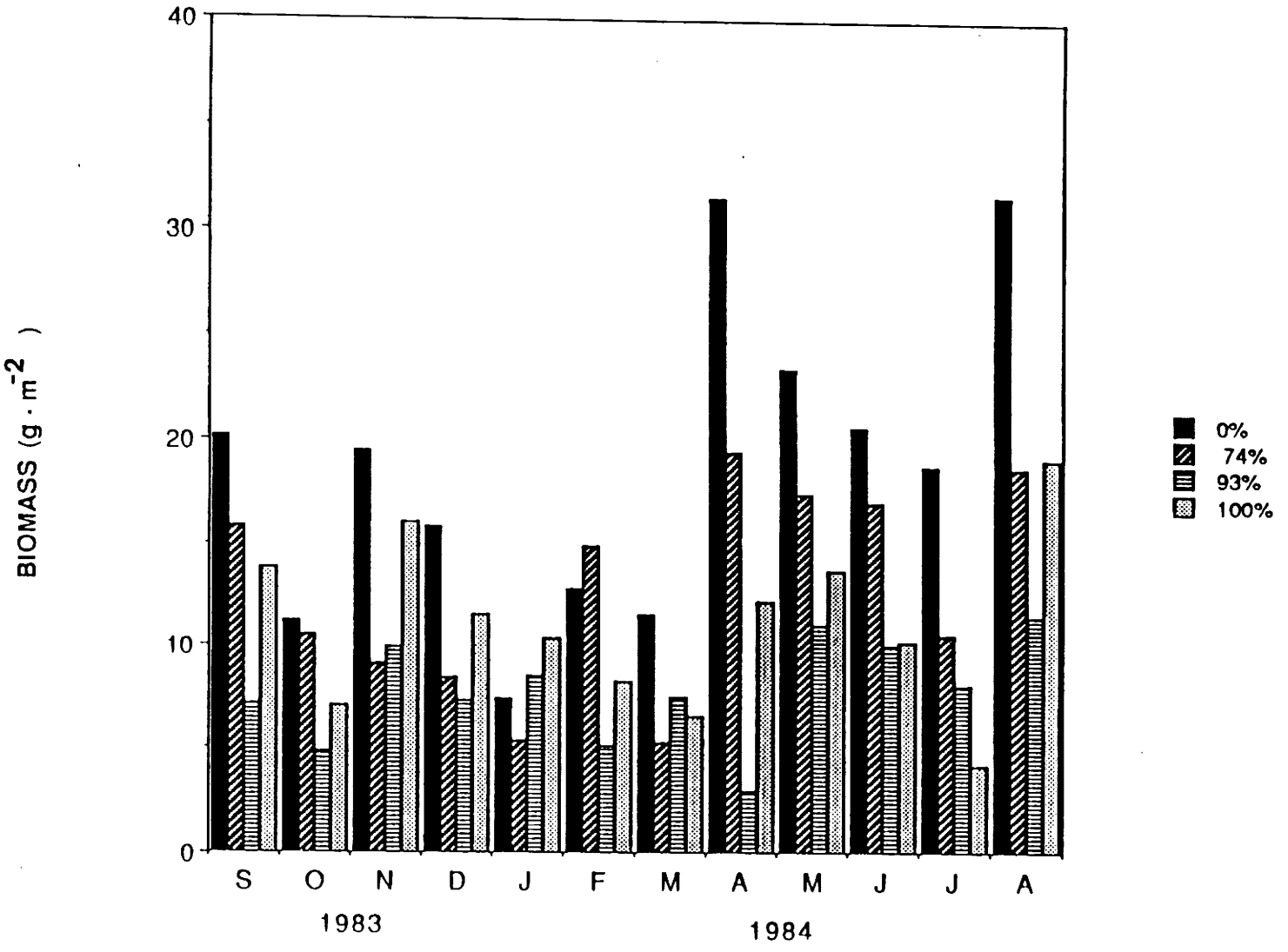

40
30
20
10
0
BIOMASS (g · m-2)
S
O
N
D
J
F
M
A
M
J
J
A
1983
1984
MONTH
0%
74%
93%
100%

Figure 2.4.

Figure 2.5. Biomass of *Juga silicula* within different shade and substrate treatments during February and July of 1985 in the diversion channel at Oak Creek, Benton County, Oregon, (Experiment III). Values are means ± 1 SE.

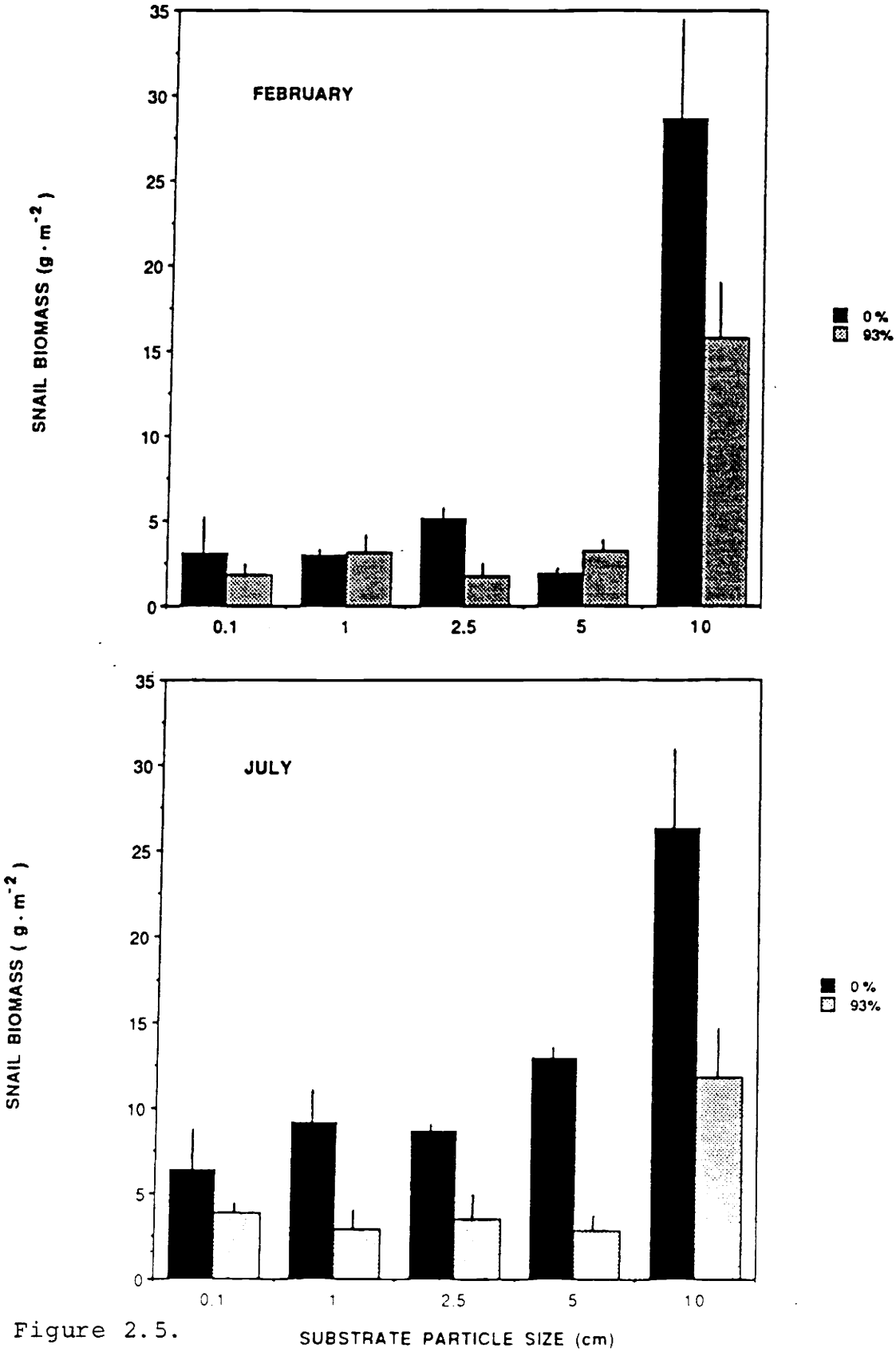

FEBRUARY
SNAIL BIOMASS (g · m⁻²)
35
30
25
20
15
10
5
0
0.1
1
2.5
5
10
0 %
93%
JULY
SNAIL BIOMASS (g · m⁻²)
35
30
25
20
15
10
5
0
0.1
1
2.5
5
10
0 %
93%
SUBSTRATE PARTICLE SIZE (cm)

Figure 2.5.

<4mm) were significantly higher in shaded treatments during September and October, but after December biomass was significantly higher in the 0% shade treatment during four of eight months (Fig. 2.6). These results indicate that a shift in shade preference from shaded to open patches occurred after the snails were a few months old.

The distribution of young snails with respect to shade was partly determined by the egg-laying site chosen by gravid females. Of the 75 egg masses collected in the June sample from the high-density population, only one was laid in the unshaded sections, and 81% were in either 93 or 100% shade (Table 2.3). The cohort hatching from these egg masses was first collected in August, 1984, when these young snails showed no clear preference for any shade treatment (Fig. 2.6).

Table 2.3. Density of *Juga* egg masses during June 1984 in the Oak Creek stream diversion channel, Benton County, Oregon within 4 shade treatments (Experiment II).

Shade (%)	Egg Masses (No.per m^2)	PERCENTAGE
0	5.3	1.3
74	68.8	17.3
93	164.0	41.3
100	158.7	40.0
Mean	99.2	

During the summer of 1985, newly hatched snails (shell length < 1mm) congregated in shaded, 1 cm substrates at a mean density of 2081 per m^{-2}, which is over three times the mean for all other treatments combined (Fig. 2.7).

Figure 2.6. Monthly density of 0+ age class *Juga silicula* with respect to shade treatments from mid-September 1983 to mid-August 1984 diversion channel at Oak Creek, Benton County, Oregon (Experiment II).

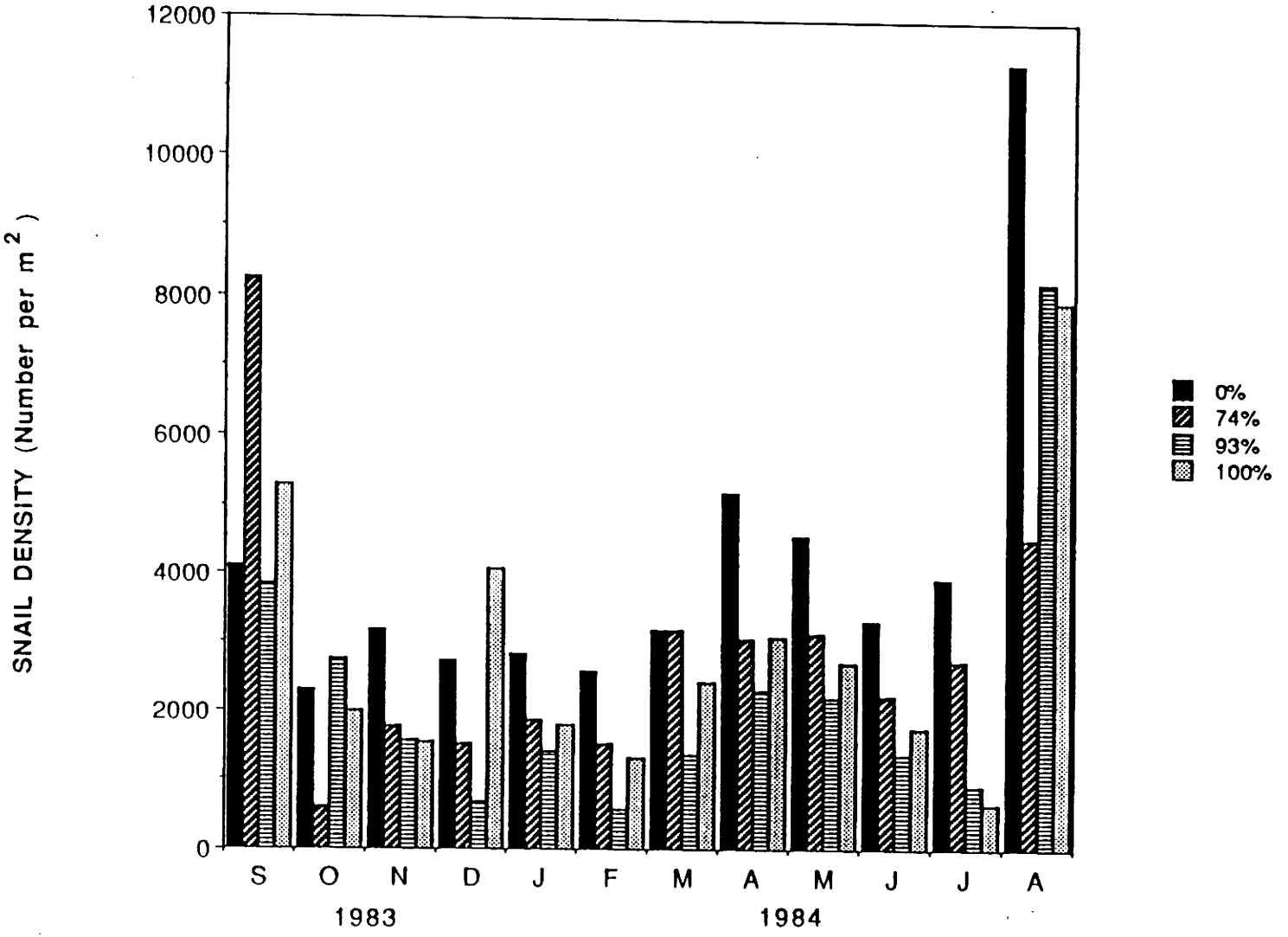

SNAIL DENSITY (Number per m 2)
12000
10000
8000
6000
4000
2000
0
S
O
N
D
J
F
M
A
M
J
J
A
1983
1984
MONTH
0%
74%
93%
100%

Figure 2.6.

Figure 2.7. Densities of 0+ size class individuals within different shade and substrate treatments during July 1985 in the diversion channel at Oak Creek, Benton County, Oregon (Experiment III). Values are means ± 1 SE.

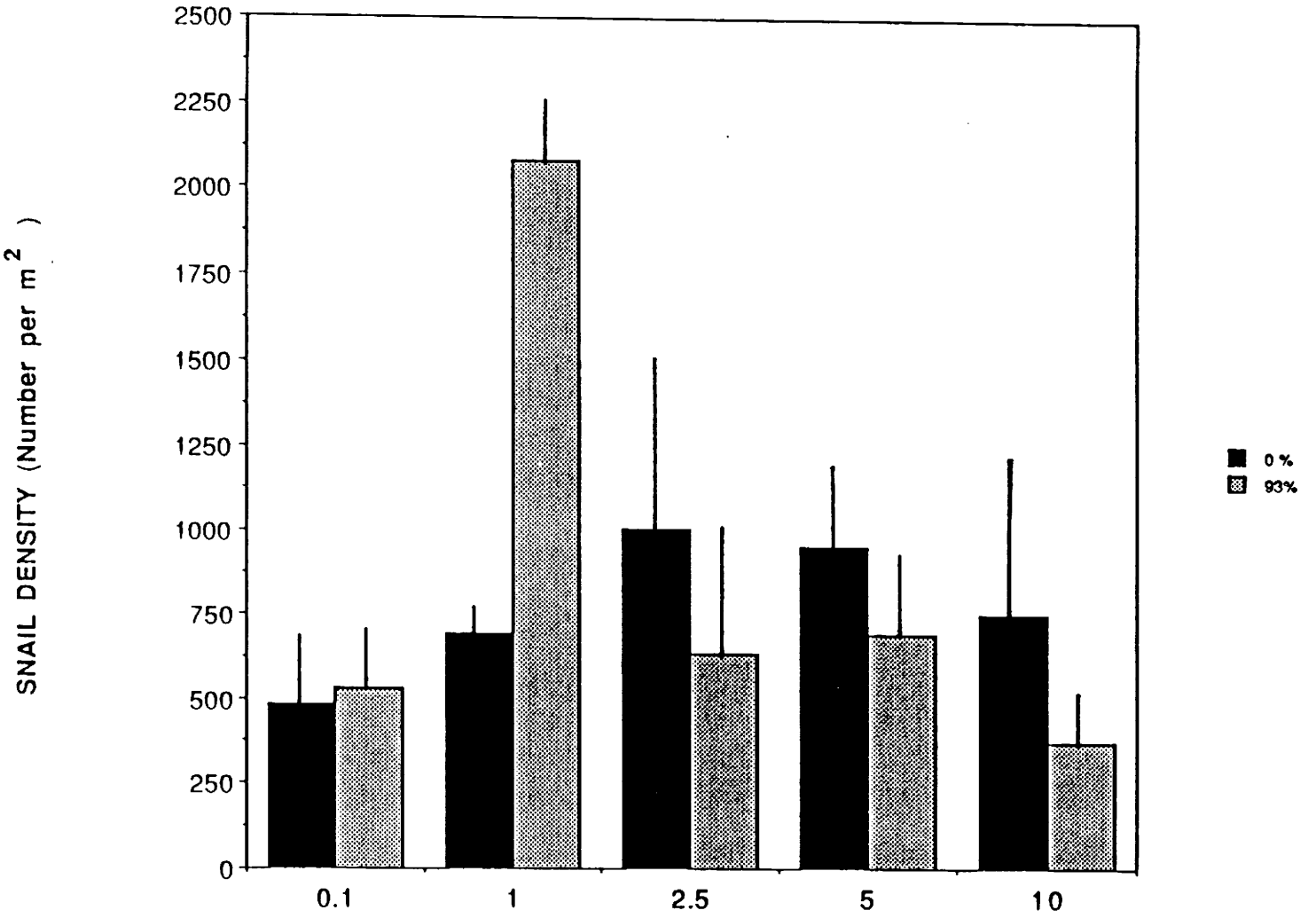

SNAIL DENSITY (Number per m 2)
2500
2250
2000
1750
1500
1250
1000
750
500
250
0
0.1
1
2.5
5
10
SUBSTRATE PARTICLE SIZE (cm)
0 %
93%

Figure 2.7.

However, analysis of variance revealed no significant treatment effect of shade or substrate on snail density (Table 2.1). Either young snails hatched from egg masses laid in 1 cm gravel or they moved to finer substrates after hatching from egg masses laid on the cobble substrates preferred by the adults. Based on observations of egg laying behavior in Oak Creek, where egg masses are customarily found attached to cobbles in riffles, the latter explanation appears to be most plausible. There appears to be no obvious explanation for the inconsistent results for the cohorts that hatched in 1983 and 1985, both of which reached highest densities in shaded sections during the first month after hatching, compared to the cohort that hatched in 1984, which showed no clear preference for any shade treatment.

Both shade and substrate influenced abundance of chlorophyll _a_, but the results were not always consistent between experiments (Table 2.1). In Experiments I and III, highest chlorophyll _a_ levels consistently occurred on 1 and 2 cm substrates (Figs. 2.8, 2.9 a,b,c). When chlorophyll _a_ was plotted against snail density in experiment I, the correlation was not significant ($R=-0.19$, $p=0.35$), however the correlation was nearly significant for biomass ($R=-0.56$, $p=0.057$).

In experiment I, substrate particle size also had a significant influence on the quantity of organic detritus >1mm collected (Table 2.1). The 5 and 10 cm substrates

Figure 2.8. Standing crop of chlorophyll *a* with respect to shade and substrate treatments on August 5, 1982 in the diversion channel at Oak Creek, Benton County, Oregon (Experiment I). Data are for the high-density snail population only.

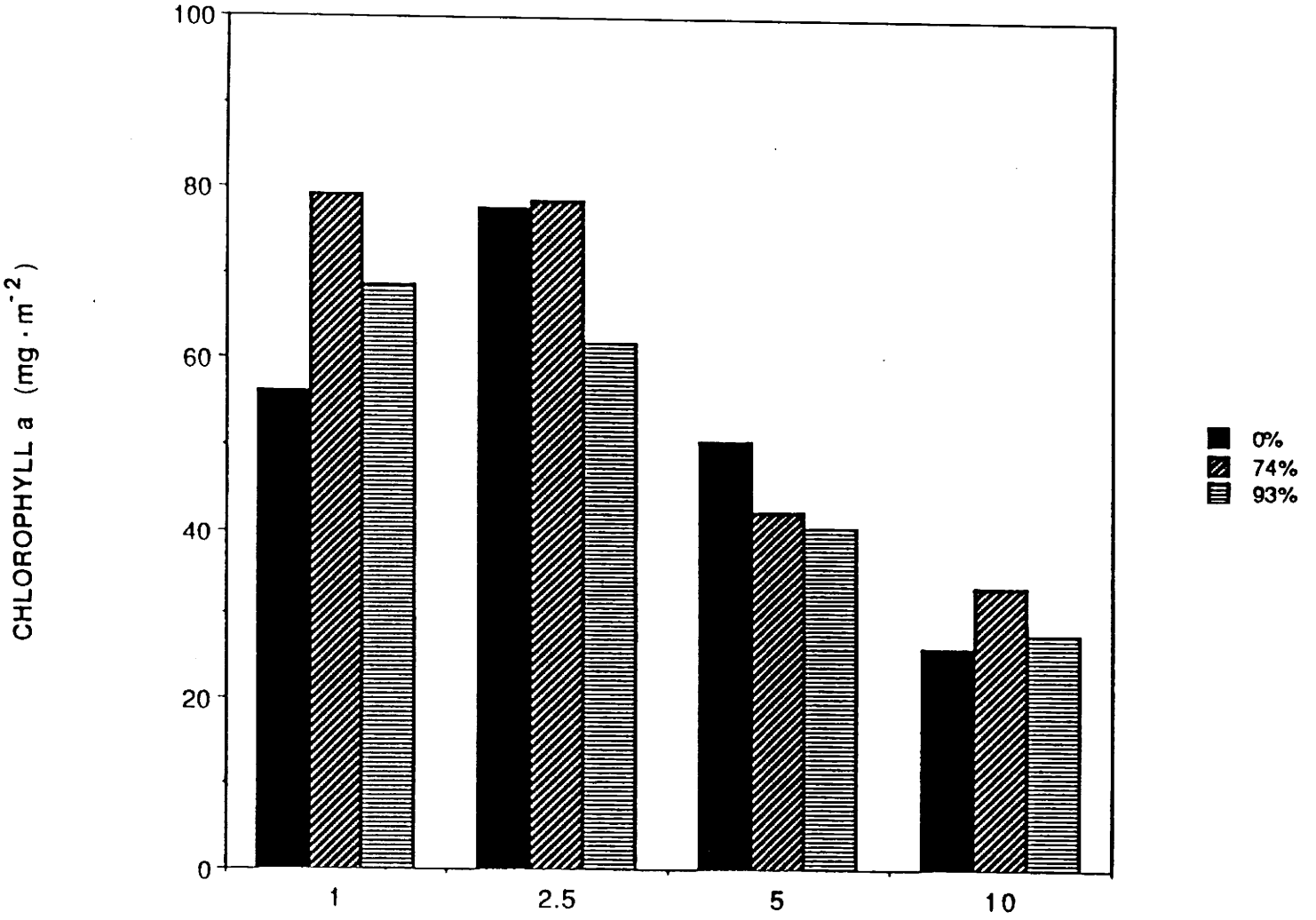

CHLOROPHYLL a (mg · m-2)
100
80
60
40
20
0
1
2.5
5
10
SUBSTRATE PARTICLE SIZE (cm)
0%
74%
93%

Figure 2.8.

Figure 2.9. Standing crop of chlorophyll a with respect to shade (%), substrate (cm diameter) and snail density (high vs. low) treatments during February, May and July of 1985 in the diversion channel at Oak Creek, Benton County, Oregon (Experiment III).

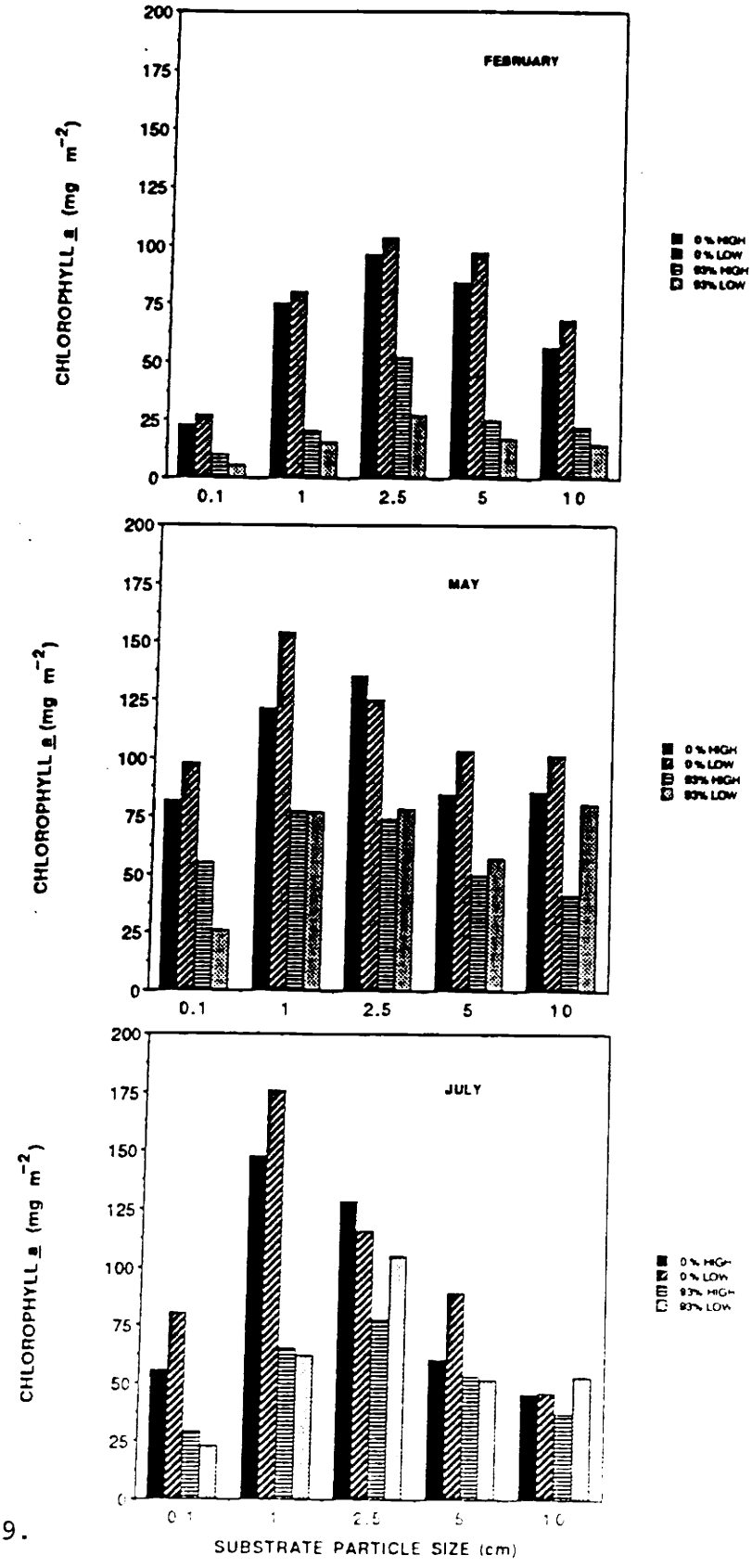

FEBRUARY
MAY
JULY
CHLOROPHYLL a (mg m-2)
0 % HIGH
0 % LOW
93% HIGH
93% LOW
0.1
1
2.5
5
10
SUBSTRATE PARTICLE SIZE (cm)

Figure 2.9.

collected more detritus than did the 1 and 2.5 cm substrates (Table 2.2). The disproportionate amount of detritus that accumulated in the heavily shaded cobble (Fig. 2.10) is not considered significant because detritus was deposited mainly in the upper (heavily shaded) portion of the artificial channel as water from Oak Creek entered it and dropped its organic load. The correlation with detritus abundance was nearly significant for both density ($R=0.26$, $p=0.067$) and biomass ($R=0.23$, $p=0.052$) of snails.

In these three experiments, although there were inconsistencies between the results generated by each, the most noteworthy item was that responses to shade and substrate particle size depended on individual size and season. The largest, oldest individuals occupied unshaded, coarse substrates. The smallest, youngest individuals occupied finer substrates and shaded habitats, at least during the first few months after they hatch. These experiments show that substrate preference by large snails was uniform over all seasons, while the tendency for large snails to congregate in unshaded areas was stronger in summer than in winter.

Hawkins and Furnish (1987) have summarized the results of a test for competition between *J. silicula* and other macroinvertebrates collected during experiment I. For the 16 most abundant taxa (93% of the total),the strength of the competitive interaction (measured as depression of abundance) was directly proportional to the degree of

Figure 2.10. Standing crop of detritus >1mm diameter with respect to shade and substrate treatments on August 5, 1982 in the diversion channel at Oak Creek, Benton County, Oregon (Experiment II).

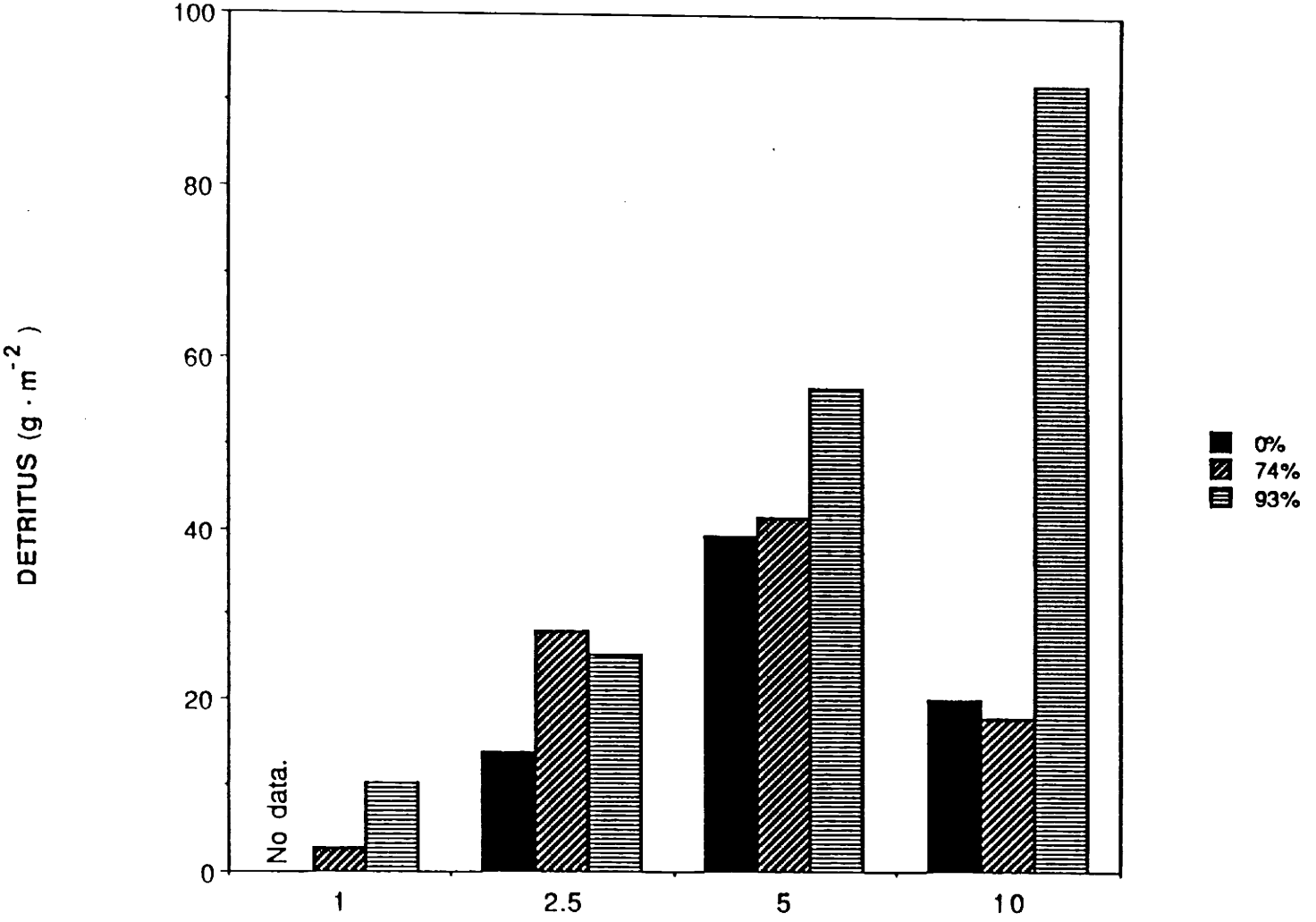

100
80
60
40
20
0
DETRITUS (g · m-2)
No data.
1
2.5
5
10
SUBSTRATE PARTICLE SIZE (cm)
0%
74%
93%

Figure 2.10.

substrate overlap between snails and other macroinvertebrates. Taxa that were mobile were affected less than those that were sedentary.

In experiment II there was good evidence that the response of some macroinvertebrate taxa to the removal of *J. silicula* depended upon season. During the winter, five taxa were uniformly depressed in abundance independent of shade treatment; during the summer, all five of these taxa shifted their distributions to shaded sections in response to a high density of snails in unshaded sections (Fig. 2.11). Similar results were observed during the summer of 1982 in experiment I for several taxa (Hawkins and Furnish 1987, Fig. 4). These taxa included, four chironomid midge genera (*Parametriocnemus*, *Micropsectra*, *Macropelopia* and *Heleniella*) and oligochaete worms. These taxa appear to have preferred unshaded sections as indicated by their distribution in the snail removal channel, but were displaced to shaded areas in August when the abundance of snails was concentrated in unshaded areas.

Field Studies

When the densities of snails were compared in different habitats, highest mean density was found in pools ($695 \pm 122 \cdot m^{-2}$) and lowest was found in cascades ($43 \pm 16 \cdot m^{-2}$, Table 2.4). However these differences were not significant (Kruskal-Wallis test, $X^2=5.36$, 5 df, NS). Biomass was also highest in pools ($9.86 \cdot m^{-2}$), and lowest in cascades ($2.55 \cdot m^{-2}$), but these differences were also not

Figure 2.11. Density ratios for five selected taxa with respect to shade during winter (mid-January) and summer (mid-July) of 1984 in the diversion channel at Oak Creek, Benton County, Oregon (Experiment II). High is the abundance of the taxon in the high-density channel and low is the abundance of the taxon in the low-density channel. Negative numbers indicate that density was highest in the high-density channel. *Cinygmula* and *Paraleptophlebia* are mayflies, *Zapada* is a stonefly, and *Stempellinella* and *Micropsectra* are chironomid midges.

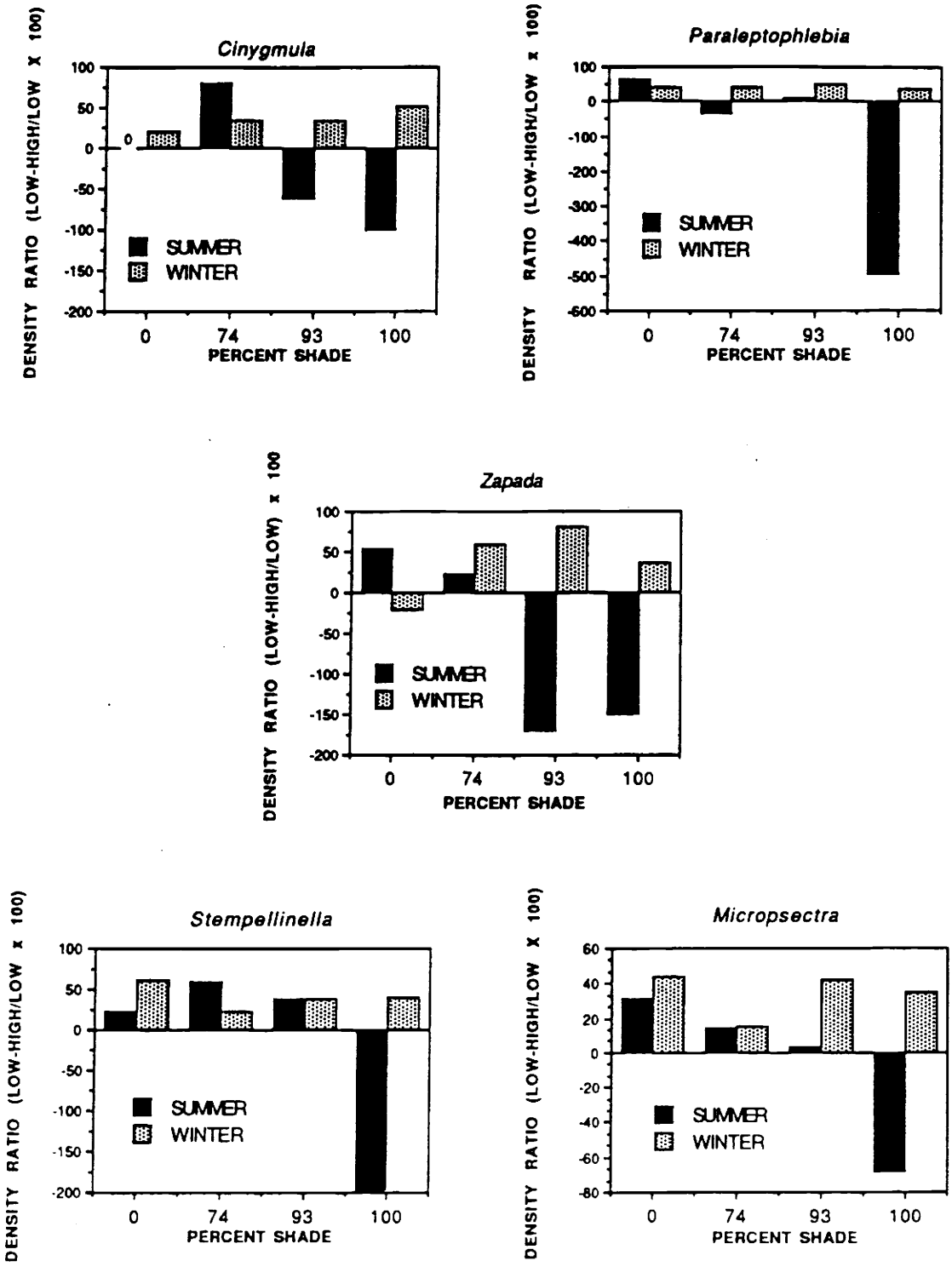

Cinygmula
Paraleptophlebia
Zapada
Stempellinella
Micropsectra
DENSITY RATIO (LOW-HIGH/LOW x 100)
SUMMER
WINTER
0
74
93
100
PERCENT SHADE

Figure 2.11.

Table 2.4. Densities and biomass of *Juga silicula* collected from six habitats in Oak Creek and Rock Creek, Benton County, Oregon during April and May, 1984. Data are presented as means ± 1 SE. and were analyzed by the Kruskal-Wallis rank sum test. NS = statistically non significant. See text for explanation of statistical tests.

HABITAT	N	CURRENT VELOCITY ($cm \cdot sec^{-2}$)	DEPTH (cm)	SNAIL DENSITY ($no \cdot m^{-2}$)	SIG	SNAIL BIOMASS ($g \cdot m^{-2}$)	SIG
POOL	28	11.9 ± 1.9	18.4 ± 2.6	695 ± 122	NS	9.86 ± 1.65	NS
BEDROCK	6	25.0 ± 2.9	23.3 ± 7.5	436 ± 74		6.91 ± 0.76	
CLAY BANK	4	25.2 ± 6.4	3.3 ± 0.7	390 ± 143		8.45 ± 3.09	
BACKWATER	4	4.0 ± 1.8	6.2 ± 0.9	355 ± 230		3.92 ± 2.20	
RIFFLE	10	22.7 ± 4.3	6.1 ± 0.6	151 ± 61		2.85 ± 0.99	
CASCADE	4	37.5 ± 5.0	13.0 ± 2.0	43 ± 16		2.55 ± 1.41	
MEAN	56	17.5 ± 1.8	14.4 ± 1.8	478 ± 73		7.25 ± 0.98	

significant (Kruskal-Wallis test, X^2=1.02, 5 df, NS).

Snail density had a highly significant negative correlation with current velocity (R=0.56, P<0.001, Fig. 2.12), but no significant relationship was found between current velocity and body size (R=0.02). Between 30-40 $cm \cdot sec^{-1}$, snail densities were always $<100 \cdot m^{-2}$ and snails were absent above 40 $cm \cdot sec^{-1}$. Current velocity alone accounts for only about 30% of the variability in snail distribution (both number and biomass), so other factors are clearly of great importance.

In both Oak Creek and Rock Creek, depth was not significantly correlated with either density (R=0.12) or biomass (R=0.10), nor were there any significant correlations with substrate particle size, probably because median particle size did not adequately characterize substrate variability.

Discussion

Size-Specific Responses

The microdistribution of *J. silicula* was size-specific and was determined by a suite of variables including light availability and substrate particle size. Large snails were most abundant on coarse unshaded, substrates (Table 2.2). Egg masses were mainly laid in shaded areas and smaller snails were most abundant in, and appeared to prefer, finer substrates ranging from 1-2 cm (Table 2.2, Fig. 2.6). After the first few months of life, there was a shift to unshaded patches which resulted

Figure 2.12. Density of *Juga silicula* with respect to current velocity. Data are for combined samples from Oak Creek and Rock Creek, Benton County, Oregon.

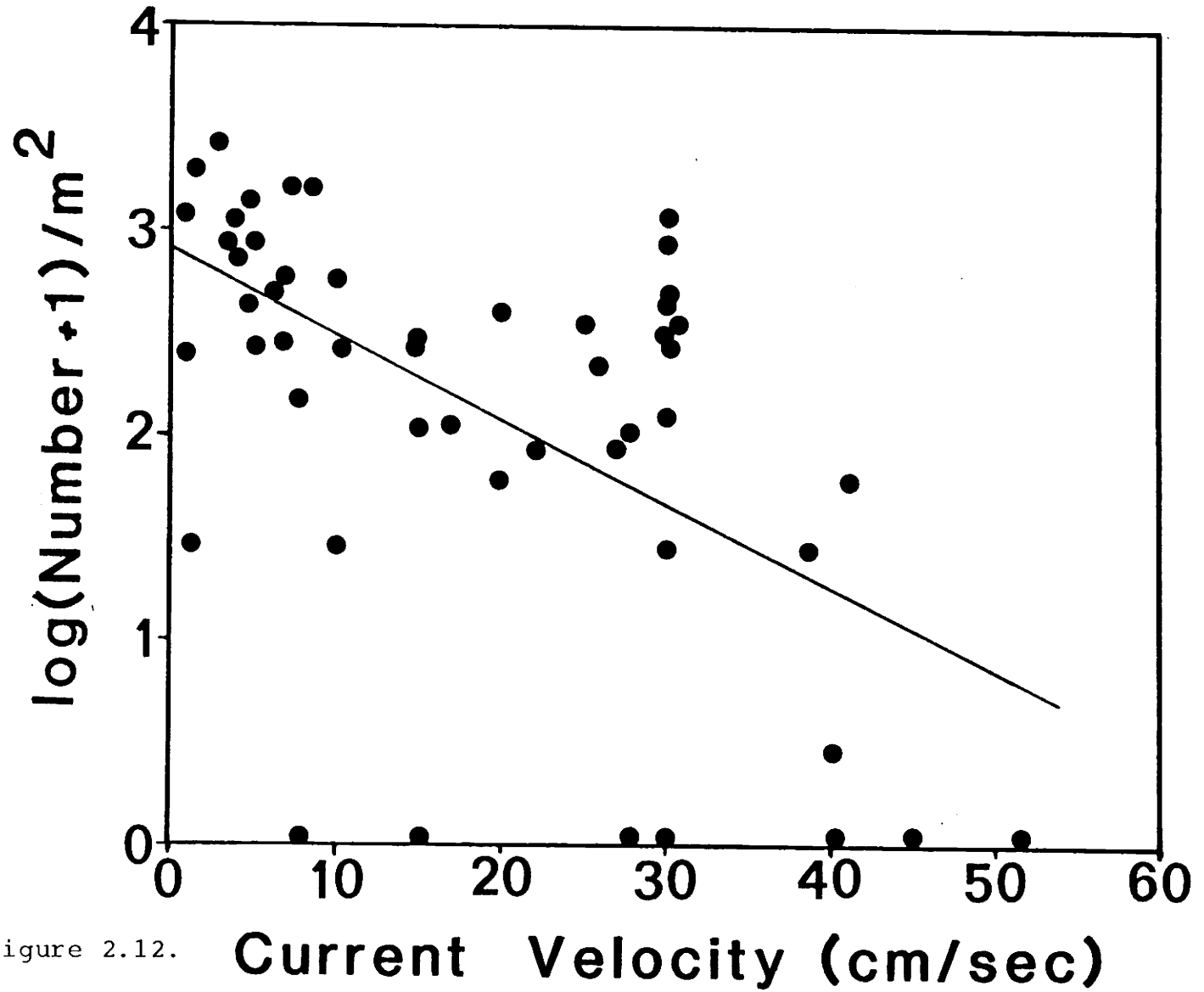

log(Number+1)/m2
4
3
2
1
0
0
10
20
30
40
50
60
Current Velocity (cm/sec)

Figure 2.12.

in a co-occurrence with larger individuals in the population.

These results are consistent with those of Diamond (1976), who reported that *J. silicula* preferred gravel and cobble over silt and sand substrates. In the Oak Creek study, it appears that the interstitial spaces of substrates in the range of 1-2 cm diameter were inaccessible to large snails because of physical constraints imposed by the small size of interstitial spaces. A similar observation and explanation has been made to account for the nonrandom distribution of *Gammarus pulex* L. (Gee 1982, Adams et al. 1987). Culp et al. (1983) observed that interstitial space was reduced by about 11% in homogeneous gravel (9.5-16 mm) compared to homogeneous pebbles (16-32 mm). In the Oak Creek study, a higher porosity was only found for cobble (Table 2.2). However, the mean size of snails on 5-cm vs. 10-cm substrates in experiment I was the same in spite of a decrease in porosity of 8%, and mean snail size was significantly smaller on 2 cm vs. 5 cm substrates even though porosity was nearly the same. Perhaps larger snails that are capable of effectively feeding on 5-cm substrates encounter some difficulty in feeding on 2-cm substrates and are not capable of exploiting the higher concentrations of food there. Regardless of the reasons for these differences, comparison of porosity within different substrates does not seem to be a useful way to

predict the mean size of snails associated with substrates of different size.

Food Effects

Even though snail density and biomass were highest on unshaded, coarse substrates, the biomass of their major food source, measured as chlorophyll a, was highest on finer substrates. These observations do not however mean that snails do not congregate in food-rich patches. There is good evidence that the gross primary production of periphyton is enhanced by both high light availability (Steinman and McIntire 1987) and moderate grazing by *J. silicula* (Gregory 1983, Lamberti et al. 1987). Gregory (1983) found that moderate grazing of the periphyton community by snails resulted in a higher assimilation efficiency (i.e. greater rate of carbon fixation per unit weight of chlorophyll a). When chlorophyll a was reduced to <50 $mg \cdot m^{-2}$, assimilation efficiency rose exponentially. Thus, the periphyton community compensates for grazing by increased production per unit of chlorophyll a. In experiment I, chlorophyll a was significantly higher on the 1 and 2 cm substrates (71-76 $mg \cdot m^{-2}$) and lowest on cobble (37 $mg \cdot m^{-2}$) where snail biomass and grazing were concentrated (Hawkins and Furnish 1987). Under these conditions, gross primary production, and consequently food availability, was probably higher than chlorophyll a levels indicate.

No significant correlation between snail density and

detritus > 1 mm was found. This result is consistent with the interpretation that periphyton is the major food source for *J. silicula*. Snails seem better adapted to grazing on hard, flat surfaces than in organic sediments.

Current Velocity

No relationship between the mean size of individuals in a sample and current velocity was found. A bimodal current velocity preference was observed by Gore (1983) for another pleurocerid snail, *Elimia potosiensis* in Oklahoma. Shell length of *E. potosiensis* declined from a mean of 13.5 mm at low current velocities (5-50 $cm \cdot sec^{-1}$) to 9 mm at velocities in excess of 100 $cm \cdot sec^{-1}$. Gore (1983) concluded that larger snails experienced unstable flows at high current velocities because their shells projected further out of the boundary layer than did the shells of smaller individuals. Perhaps the lack of a correlation between current velocity and mean shell length is in part explained by the lower range of current velocities used in this study. Statzner et al. (1988) reported that for the mudsnail *Potamopyrgus* (Hydrobiidae), there was a significant correlation between viscous sublayer thickness (which is directly proportional to current velocity), and mean shell length only during the summer season when most of the large individuals were at or near the substratum surface. In the diversion channel, *J. silicula* was also most abundant at the substratum surface during the summer (personal observation). It is

therefore possible that the lack of a significant correlation was due to the fact that field samples were taken in the spring when snails were mainly distributed below the substrate surface where they would not have been directly affected by current velocity.

Effects of Physical Variables on Competitive Interactions

The influence of substrate particle size on competitive interactions between *J. silicula* and aquatic insects has been demonstrated by Hawkins and Furnish (1987). Competitive displacement of some aquatic insects by snails was directly proportional to the amount of overlap in resource use. In the study presented here, there is a strong suggestion that the intensity of competition between snails and aquatic insects is also dependent upon season and shade (Fig. 2.11). The decline in abundance of snails at current velocities greater than 30 $cm \cdot sec^{-1}$ also implies that the potential intensity of competition declines with increasing current velocity. The degree to which other macroinvertebrates can avoid competition with snails depends upon their ability to occupy areas were snail abundance is reduced.

CONCLUSIONS

The results reported here show that shade, substrate and current velocity strongly influence the distribution of *J. silicula*, the former two factors operate in a size-dependent manner. The contrasting microhabitats occupied by snails of different size classes allows the population

to utilize a broad range of available microhabitats allowing snails to avoid intraspecific competition and reach high abundances in many streams. The season-specific response to shade by *J. silicula* results in a shade-specific response by some aquatic insect taxa to competition with snails in the summer, but not in winter.

CHAPTER III

DENSITY-DEPENDENT GROWTH, PRODUCTION AND DISPERSAL OF THE STREAM SNAIL, *Juga silicula*

ABSTRACT

Mark-recapture methods were used to compare monthly growth, dispersal, and annual production of the stream snail, *Juga silicula* at two population densities in a stream diversion channel. When standing-crop biomass was reduced by a factor of six, individuals grew faster and the production-to-biomass (P/B) ratio was increased by a factor of almost five in the low-density population. Individuals in both populations were inactive and lost weight during the winter when stream temperature was 5°C or less. Grazing by snails in the high-density population significantly reduced standing crops of chlorophyll a during 7 out of the 9 months when snails were active. Monthly growth rates were correlated with water temperature and chlorophyll a standing crop.

J. silicula is a food generalist; when offered a range of foods in the laboratory, it grew best on periphyton. Growth was also positive on carrion, alder leaves and conditioned wood. Laboratory growth rates were highly correlated with carbon:nitrogen ratios. In the laboratory, snails reached the size of a sexually-mature adult in three years (i.e. shell length of 15 mm).

High rates of dispersal were associated with high snail density, warm temperatures and low food availability. Individuals in the high-density population had significantly higher rates of dispersal than those in the low-density population during the fall, spring and

summer. Snails were positively rheotactic in both populations. These field studies show that grazing activity by *J. silicula* significantly reduced chlorophyll a standing crops in a stream. As a result, the snail's per-capita growth and production also were reduced.

INTRODUCTION

Although there have been a number of studies on growth and secondary production of benthic macroinvertebrates (reviewed by Waters 1977, Benke 1984, Downing and Rigler 1984), most have been descriptive rather than experimental. Long-term studies of stream production have revealed that there is a great deal of variability between years (Illies 1975), but the reasons for this variation are not clear. This condition is an impediment to understanding the factors that determine production in stream communities. As Downing (1984) has pointed out, production ecology has a great number of hypotheses, but few have been tested explicitly. Secondary production is dependent upon physical factors such as temperature (Laville 1971, Neves 1979) and water quality (Krueger and Waters 1983), but the importance of biological factors, such as food availability and competition, is poorly known.

In this study, factors affecting the growth and distribution of the stream snail, *Juga silicula* (Gould) were examined. Observations were made on growth and dispersal of two stream populations. In an experimental study conducted in a diversion channel, snail density was manipulated to determine whether growth, annual production and dispersal were density-dependent. Growth of a lab population over three years was monitored to determine the relationship between age and size. Laboratory growth on a

variety of different foods was also measured to examine the influence of food quality on growth.

METHODS

Field Studies

Snail populations from Oak and Rock Creeks, Benton County, Oregon were studied from 1983-1985. The Oak Creek site, located 10 km northwest of Corvallis, is a third-order stream that drains the eastern foothills of the Coast Range at an elevation of 154 meters. The Rock Creek site is on the east side of Marys Peak in the Coast Range at an elevation of 205 meters. Further details on the physical habitat of the streams are given in Chapter I.

Studies were conducted at Oak Creek in a concrete diversion channel that had been used to manipulate physical variables and snail densities in past experiments (Hawkins and Furnish 1987). The channel was 48 meters long, 0.9 m wide and 0.9 m deep, with a slope of 2%. It was divided length-wise with rough-cut lumber to create two experimental streams. River gravel (5 in cm diameter) was added to the channel to a depth of 10 cm and vertical wooden dividers 20 cm high were pushed into the gravel every 1.5 meters to brace the center divider and impede the force of the current. This design created a stair-step pair of streams, each with a mean current velocity of 15 $cm \cdot sec^{-1}$ and a discharge that was generally maintained at 0.03 $m^3 \cdot sec^{-1}$ by adjusting the amount of water passing through a gate at the upstream end. When the creek was at

flood stage, discharge increased 2-3 fold but these events were of short duration.

Four shade treatments (0, 74, 93 and 100%, see p. 25 for details) were used to vary the amount of light reaching the stream. Each treatment covered two sections for a total length of 3 m. The four shade treatments were randomly ordered within each of three blocks along the length of the channel for a total of 12 3-meter sections.

In July of 1983, snails were collected from Oak Creek and Berry Creek (located 11 km to the north in the foothills of the Coast Range). They were added to the east side of the experimental channel at a mean density of 13.3 g total body ash-free dry mass (AFDW)$\cdot m^{-2}$, which is within the range of densities commonly observed for *J. silicula* in Oak Creek and other streams (Gregory 1980, Diamond 1982, Hawkins and Furnish 1987). This group of snails constituted the "high density" population.

The west side of the channel was not seeded, with the intention of completely excluding snails from that side, but this proved to be impractical as immigration from the high-density population was extensive. This condition made it necessary to remove snails every 3-4 days by hand picking. A mean snail density of 2.1 g AFDW$\cdot m^{-2}$ (16% of that in the high-density population) was maintained on the low-density side from August 1983 through August 1984.

Chlorophyll a standing crop was measured monthly to estimate food availability. For each sample, three stones

were collected from each section, for a total of 36 samples from each experimental stream. Samples were placed in plastic bags and stored on ice in a cooler until they could be returned to the lab. Samples were frozen and extracted in 90% buffered acetone for 24 hours. Concentrations of chlorophyll *a* were measured with a spectrophotometer and calculations were made according to the methods of Lorenzen (1967) and Marker and Jinks (1982). Differences between samples were assessed by paired t-tests.

During the spring of 1984, the relationship between chlorophyll *a* and aufwuchs biomass, as a measure of the food available to each snail population was also determined. Ceramic tiles (7.5 x 1.5 x 1 cm) were placed parallel to the current and exposed to colonization from March 16 to May 14. Two tiles were placed in each section. After the colonization period, the tiles were retrieved and chlorophyll *a* concentrations measured by the methods given above. The aufwuchs on the second tile from each section was scraped off with a razor blade and its ash-free dry weight was determined by measurement of weight loss by combustion at 550^{o}C. A total of 12 chlorophyll *a* and biomass samples were taken from each stream with three paired replicates from each shading level.

The impact of snails on periphyton community composition was examined in the fall of 1984. Using the

same tile arrangement, the effect of snail grazing was measured by comparing periphyton species richness, cell density and taxonomic composition in the diversion channel streams after 40 days of colonization (October 3 to November 12). Tiles were retrieved from the stream, placed in bags on ice until they could be taken to the laboratory for analysis. All the samples from each stream were pooled for analysis.

Standing crop of snails was measured with a Hess sampler (0.02 per m^2, mesh size 250 μm). Each month, 36 samples (12 sections x 3 replicates) were taken from each population. The following month, samples were taken from the alternate section within a shade treatment so that two months passed before a particular section was resampled. With the exception of January, 1984, the nine samples from each shade treatment were combined to facilitate sample processing.

During a second experiment that lasted for 434 days (August 14, 1984 to October 31, 1985), the channel was restocked and the positions of the high and low-density populations were switched. Mean densities over the second study period were 26.5 and 5.1 g AFDW$\cdot m^{-2}$ (low=19% of the high). Growth and dispersal of individually marked snails was monitored for 177 days, from April 10 to October 4, 1985.

Shell lengths of the snails in each sample were measured to the nearest millimeter. Shell and tissue AFDW

were determined by measuring weight loss after combustion at 550°C for 4 hours. Units of total body weight (tissue + shell) were adopted because snail growth includes allocations to shell secretions as well as to soft tissue (Russell-Hunter and Buckley 1983). The shell is composed of an organic matrix of protein fibers, including the periostracum, and crystalline calcium carbonate. Biomass is expressed as "total body" ash-free dry weight which includes the combustible organic component in the shell (5.8 ± 1.5% of shell dry weight). This method also avoided errors due to incomplete removal of tissue when extracting snails from their shells. When partitioning of body weight between soft body parts and shell was desired, snails were sacrificed by immersion in boiling water and cooled in a refrigerator for a few hours to facilitate tissue extraction. Conversions between shell length (SL) in cm and biomass units (mg) were made using the following formulae:

$$\text{Total Fresh Wt.} = 85.736\ (SL)^{2.58},\quad n=30,\ r^2=0.93 \qquad (3.1)$$

$$\text{Total AFDW} = 8.1338\ (SL)^{3.097},\quad n=30,\ r^2=0.96 \qquad (3.2)$$

$$\text{Total AFDW} = 0.1197\ (\text{Fresh Wt.}),\quad n=36,\ r^2=0.86 \qquad (3.3).$$

Sex was determined by examination of the gonads and by presence or absence of a genital sinus. This occurs as a distinct, light-colored groove on the right side of females when they reach sexual maturity (Ching 1957, Dazo 1965, Diamond 1977). The sex of snails greater than 13 mm shell length or 150 mg fresh weight could usually be

determined by this method. Individuals greater than 150 mg fresh weight, with no evidence of a genital sinus were scored as males.

Growth of marked snails was monitored monthly in the experimental channel from August 1983 to August 1984, and in the spring and summer of 1985. A numbered bee tag (Chr Graze KG, Weinstadt, West Germany) was attached with super glue and the snail with tag was weighed to the nearest 0.01 mg. In August 1983 and April 1985, 100 and 200 marked individuals were released in the low- and high-density populations, respectively. Each month the stream was searched for about 1-2 hours on three consecutive days for marked snails. All individuals recovered from each population were taken into the lab and reweighed to calculate specific growth rate (Kaufmann 1981). The formula used was:

SGR =(Fn Wt-In Wt)/((Fn Wt+In Wt)/2)/Days Elapsed. (3.4)

where SGR = Specific Growth Rate, Fn Wt = final fresh weight, and In Wt = initial fresh weight.

Evaluation of growth by this method is very useful for organisms like *J. silicula* that cannot be accurately aged and have many cohorts present in the population at any given time. Specific growth rates were linearized by log transformation (Kaufmann 1981). Degree days accumulated for each growth period were calculated based on a threshold temperature of 4°C, which was observed to be a good approximation of the temperature at which snail

growth ceased.

Growth rates of marked snails in Oak Creek were also measured during the spring and summer of 1984 and 1985, and in Rock Creek during the spring and summer of 1984. One hundred marked snails were released into Oak Creek each year. In Rock Creek, 50 marked snails were released into a sunny, shallow pool and 100 were released into a shaded riffle area 100 m upstream.

Secondary production was determined for both snail populations in the diversion channel using the instantaneous growth method (Rigler and Downing 1984). This method assumes that growth is exponential within a size class. It was calculated for each month by the following formula:

$$P = \Sigma (B_i G_i) \qquad (3.5)$$

where P= Production, B_i= mean biomass of size class i, G_i= specific growth rate of size class i (range of 0.5 to 25.5 mm).

If the slope of log-transformed growth vs. initial size was significantly different from 0 and accounted for a significant degree of the variability in growth rate (i.e. $r^2>0.20$), monthly production was calculated by summing the products of estimated growth for each size class, based on the regression equation and standing crop. If the slope did not account for significant variability in growth, monthly production was calculated as the product of mean growth rate for the recaptured population

and total standing crop of snails. The sum of monthly production over 12 months equals annual production.

Production is defined as "the amount of tissue elaborated, ...regardless of its fate" (Downing 1984). Thus, a net weight loss recorded for a snail population was recorded as negative production since the weight lost was attributable to tissue elaborated at some prior time whether it was allocated to reproduction, degrowth (i.e. a decrease in the mass of structural proteins during the winter months, Russel-Hunter et al. 1984), or lost to predation.

Manipulations of snail density could not be replicated because only one channel was available. As a consequence of this pseudoreplication (sensu Hurlbert 1984), it is possible to test for differences between samples from each channel but the differences cannot unequivocally be attributed to treatment effects (see Hawkins and Furnish 1987). Significant regressions of monthly growth rate vs. size in the high- and low-density populations were compared by ANCOVA (Snedecor and Cochran 1982). When there was no significant regression, monthly growth rates were compared by t-tests, or Mann-Whitney U-tests if data could not be normalized or variances were heterogeneous.

Dispersal behavior of snails in the diversion channel was examined by determining distances moved by marked individuals, and also by measuring the number of snails

that accumulated in the gate area (i.e. snails were positively rheotactic and congregated in the gate area after dispersing upstream). Individual rates of dispersal were measured by calculating distance moved between successive recaptures, divided by the number of days elapsed. Estimates were usually made two times each week. Monthly dispersal by individuals in each population was compared using Mann-Whitney U-tests (Sokal and Rohlf 1981). Dispersal by marked individuals in Oak and Rock Creeks was measured weekly for 80 days during the summer. Rates of dispersal were compared using the same statistical methods as before. Snails were collected from the gate area with a dip net and total number was estimated volumetrically. Counts made using this technique were consistently within 10% of actual counts. Nets were placed in the channel inlet and outlet from mid-September to mid-October to estimate immigration and emigration, respectively. The nets collected relatively few snails and movements by marked individuals were nearly always upstream. It was therefore concluded that movement of snails into and out of the channel from Oak Creek was negligible most of the year. Infrequent flood events may have deposited some snails in the channel.

Laboratory Studies

Two studies on the growth rate of *J. silicula* were conducted in the laboratory. In a long-term rearing project, the goals were to determine the time required for snails to reach a mature size and to measure growth rate for a single cohort. The second study, which was 7 weeks long, was designed to evaluate the effect of food quality on snail growth.

Snails were reared at the Oak Creek Aquatic Entomology Laboratory in wooden artificial streams described by Brocksen et al. (1968). The lab roof was made of semi-transparent plastic that admitted some sunlight. Ambient light was supplemented for 12 hours daily by a fluorescent light hung 1 m above the stream surface. Sand-filtered spring water was delivered to each stream at a rate of 1 $l \cdot min^{-1}$, and was maintained at a depth of 10 cm. Paddle wheels driven by electric motors produced a current velocity of 5 $cm \cdot sec^{-1}$. Algae growing on the walls of the stream provided the major food source but tiles coated with a thick growth of diatoms (mainly *Synedra ulna*) were sometimes added as a supplement. The lab population was initiated with 20 egg masses that hatched between June 10 and June 24, 1983. The snails were reared at ambient temperatures (range 5-15°C) except during winter, when a heating coil was placed in the stream to prevent freezing. Growth was measured as increase in shell length and dry weight.

Growth rates on a variety of food types were determined for 2-year-old snails. In spite of their uniform age, the variation in sizes necessitated a division of the snails into three groups: small (shell length, 5-7 mm; fresh weight, 15-34 mg), medium (7-10 mm; 35-85 mg) and large (10-15 mm; 86-244 mg). Six snails, 2 from each size class, were placed in a plastic tray (22 x 22 x 7 cm) together with a selected food treatment. Trays were then covered with a 1-mm screen and submerged in two artificial streams. This design yielded 8 replicates for each size class and food type (2 streams x 2 food replicates/stream x 2 snails from each size class/tray). Temperatures ranged from 10-15^{o}C during the experiment which lasted 7 weeks (May 22 to July 10, 1985).

Six food types were used in the feeding experiments: 1) periphyton grown on a tile (225 cm^2) from an ungrazed stream; 2) carrion composed of 18 orange tortrix (*Argyrotaenia citrana* (Fernald)) larvae submerged live at the beginning of each food addition; 3) three alder leaves leached for 48 hours; 4) conditioned wood, 15 cm long and 3 cm dia. collected from Oak Creek; 5) 25 cm^3 of sieved (106-250 um) sediments from Oak Creek, including sand and fine particulate organic matter (FPOM); and 6) a combination of all of the above foods each offered in reduced quantities. An additional set of 4 trays without food served as a control group. These trays were washed out at least once every week and there was no algal growth

observed on them during the course of the experiment. The control group of snails had a positive growth rate even though they were given no food. This phenomenon was attributed to low densities of periphyton growing on the trays and fine organic particles, comprised of dislodged algae and bacteria that were deposited in all the trays. All food treatments should then be considered as supplements to this diffuse food source that sustained a relatively low level of positive growth in the control group over the 50-day experiment.

The food in each tray was replenished weekly (twice each week for orange tortrix larvae). It is assumed that all foods were provided in excess as there was no evidence that any food was depleted within a week .

At the end of the experiment, food samples were dried and combusted to determine ash-free dry mass. Percent carbon and nitrogen were determined with a Carbo Erba Elemental Analyzer by the Department of Biology, Idaho State University. Percent carbon and nitrogen were also determined for aufwuchs samples taken from the diversion channel streams during January and August of 1984.

Laboratory growth rates on different foods were compared by single classification analysis of covariance, using initial weight as the covariate. A posteriori comparison of mean growth rates were made using Student-Newman-Keuls multiple range tests.

RESULTS

Field Studies

Size Distribution-Density Relationships

The size distribution of the snail populations in the diversion channel differed from that of a natural population because the initial stocking of the channel mainly included mature individuals. As a result, for the high-density population, the mean density of snails in size class II (shell length 5-10 mm) was lower than the mean density in size class III (shell length 10-15 mm, Table 3.1). Mean density of snails in size class I (shell length 0-5 mm) was nearly the same in both populations indicating that recruitment from egg masses in September was similar in spite of a 5-fold difference in total biomass for those populations.

Mortality of newly hatched snails was very high during the first month for both populations (Table 3.1). Starting from an initial population density of 4800-4900 per m^2 in September, only 1450-1500 per m^2 remained in October, which represents a survivorship of only 30-32% after one month. The gradual increase in density of size class I (0+ age class) snails from December to April is probably the result of flooding in Oak Creek which could have deposited large numbers of very small snails in the channel. For example, in February one major flood washed

Table 3.1. Mean density for five size classes of *Juga silicula* in the high- and low-density populations from September 1983 to August 1984 in the Oak Creek diversion channel, Benton County, Oregon. Data are expressed as number per m^2. Initial stocking of snails was in July of 1983.

		SIZE CLASS					
		I	II	III	IV	V	
		SHELL LENGTH (mm)					
MONTH	DENS	0-5	5-10	10-15	15-20	20-25	TOTAL
SEP 1983	HIGH	4794	163	197	211	13	5378
	LOW	4935	83	55	48	0	5121
OCT	HIGH	1516	103	167	124	0	1910
	LOW	1466	7	16	3	0	1492
NOV	HIGH	1366	179	257	191	5	1998
	LOW	1236	43	16	7	0	1302
DEC	HIGH	1797	79	201	166	5	2248
	LOW	1094	12	16	5	0	1127
JAN 1984	HIGH	1658	48	142	121	5	1974
	LOW	1869	12	3	2	0	1886
FEB	HIGH	1172	31	154	177	3	1537
	LOW	2299	27	53	32	0	2411
MAR	HIGH	2149	123	156	107	1	2536
	LOW	1381	36	17	26	1	1461
APR	HIGH	2178	285	428	322	10	3223
	LOW	2578	73	59	44	0	2754
MAY	HIGH	2247	303	371	209	11	3141
	LOW	1530	52	32	11	0	1625
JUN	HIGH	1398	230	342	181	1	2152
	LOW	1097	35	32	20	0	1184
JUL	HIGH	1429	228	288	108	2	2055
	LOW	926	63	39	26	0	1054
AUG	HIGH	7004	415	328	272	12	8031
	LOW	3991	336	128	94	5	4554
MEAN	HIGH	2392	182	253	182	6	3015
DENSITY	LOW	2034	65	39	27	0.5	2164
% OF	HIGH	79	6	8	6	0.2	100
MEAN	LOW	94	3	2	1	0*	100

*<0.1%.

through the channel with enough force to move some of the gravel and to deposit noticeable quantities of sand. In spite of these problems, the data for the first three to four months in Table 3.1 appear to provide an adequate representation of the mortality curve for the cohort that hatched in 1983.

Even though the abundances of snails in the two channel populations were similar because of similar recruitment of young snails, the biomass of the low-density population was only 16% of that of the high-density population. This difference resulted in a much greater impact on the periphyton food resource in the high-density population compared to that in the low.

Chlorophyll a and Aufwuchs Standing Crops

Standing crop of chlorophyll a varied with month and snail density (Table 3.2), as well as with shade (see Chapter II). Standing crop was generally lower from November to March than in the warmer months. In the high-density population, standing crop exceeded 100 $mg \cdot m^{-2}$ only once, while in the low-density population, chlorophyll a standing crops were greater than 100 $mg \cdot m^{-2}$ during 7 out of 13 months.

Chlorophyll a and aufwuchs biomass were significantly lower in the high-density channel than in the low-density channel during the spring of 1984 (Fig. 3.1). In unshaded

Table 3.2. Summary of degree days accumulated each month, mean monthly chlorophyll a standing crops (averaged over all shade treatments) and growth rates of marked snails in the high- and low-density diversion channel streams at Oak Creek, Benton County, Oregon from September 1983 through August 1984. High and low dens. refer to snail population density. Means are calculated for 12 months (Sept. 1983 to Aug. 1984). Data are presented as mean ± 1 SE. Significance levels determined by paired t-tests for chlorophyll a, and t-tests or Mann-Whitney U-tests for growth data. (*=P<0.05, **=P<0.01, ***=P<0.001, n=36 for all chlorophyll a data.)

	DEGREE	CHLOROPHYLL a($mg \cdot m^{-2}$)			GROWTH RATE($mg \cdot g^{-1} \cdot day^{-1}$)				
MONTH	DAYS	HIGH DENS.	LOW DENS.	SIG.	N	HIGH DENS.	N	LOW DENS.	SIG.
JUL	ND[1]	43.0±19.70	44.2±10.8	ns	No snails.		No snails.		
AUG	ND[1]	83.9± 5.13	101.7± 5.75	*	Not Measured.		Not Measured.		
SEP	224	99.1± 5.35	123.4± 5.30	**	33	0.97± 0.31	61	3.25± 0.40	**
OCT	247	104.4± 5.16	125.8± 6.31	*	12	1.13± 0.28	37	2.69± 0.29	**
NOV	236	71.0± 5.90	89.4± 8.15	ns	22	0.24± 0.19	32	1.37± 0.16	***
DEC	129	56.9± 5.96	87.5± 7.75	**	18	0.09± 0.16	24	0.02± 0.18	ns
JAN	60	81.8± 8.93	82.2± 9.13	ns	14	-0.16± 0.18	21	-0.25± 0.18	ns
FEB	86	47.7± 6.71	56.7± 8.33	ns	20	-0.20± 0.24	28	0.41± 0.22	ns
MAR	110	66.2± 7.45	83.6± 9.16	ns	18	-0.06± 0.21	28	0.56± 0.19	ns
APR	147	75.3± 5.80	131.2±12.86	**	31	0.13± 0.10	26	1.00± 0.20	***
MAY	165	96.9± 6.26	157.5±17.90	**	30	0.31± 0.13	22	1.14± 0.30	*
JUN	235	87.5± 8.90	133.6±11.45	***	27	1.10± 0.24	17	1.18± 0.37	ns
JUL	271	77.9± 6.77	94.5± 8.73	ns	20	0.12± 0.32	12	0.82± 0.52	ns
AUG	253	88.9+ 6.90	115.7+ 9.90	**	29	-0.12+ 0.22	20	0.69+ 0.28	*
MEAN[2]		79.8	106.3			0.30		1.07	

1) ND= Not determined.
2) From September 1983 to August 1984.

Figure 3.1. Aufwuchs biomass (above) and chlorophyll *a* concentration (below) at four shade levels and two snail densities in the diversion channel at Oak Creek, Benton County, Oregon. High is for the high-density channel and low is for the low-density channel. Tile substrates were colonized for 60 days (March 16 to May 14, 1984). Data are presented as means ± 1 SE.

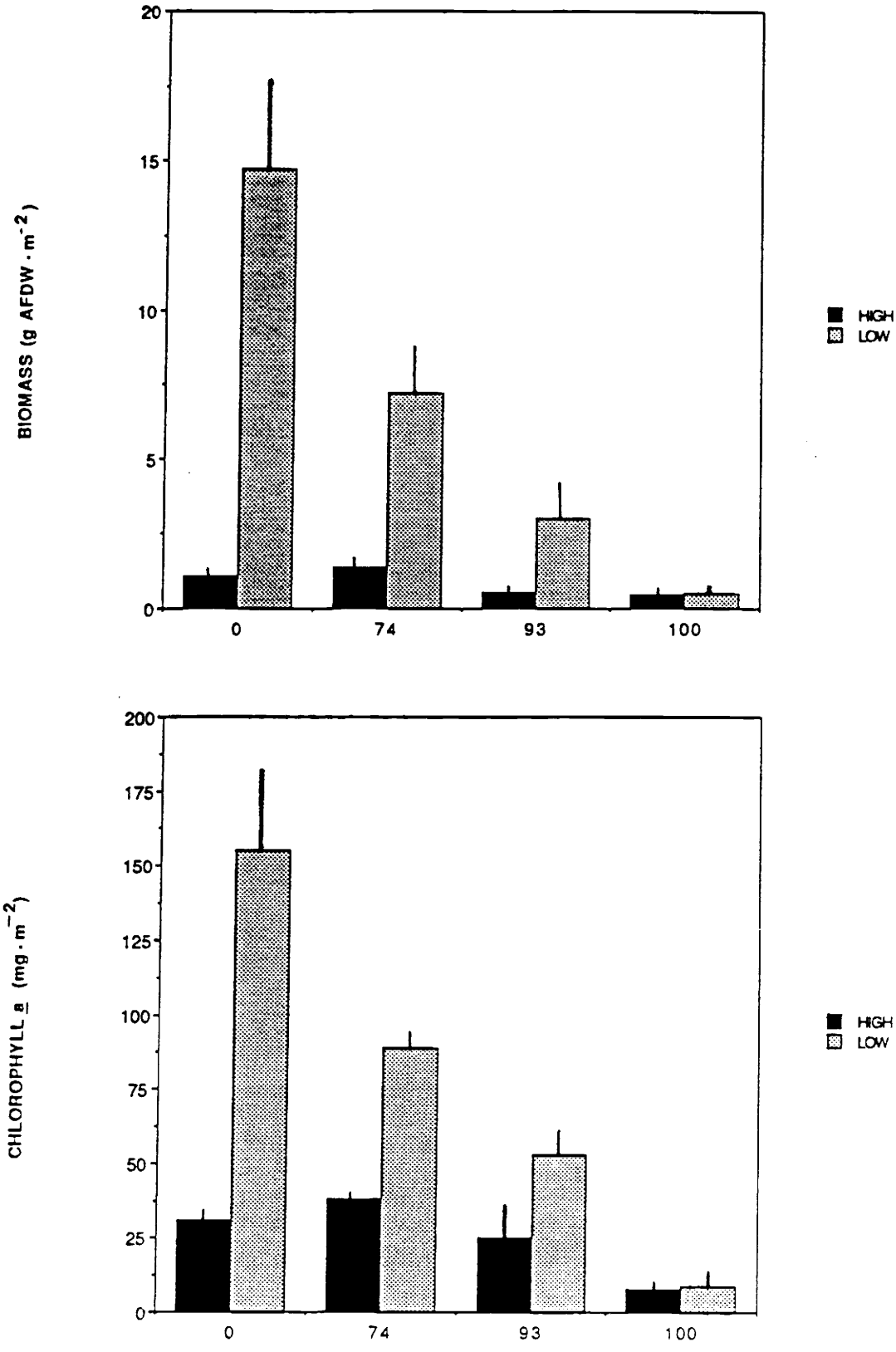

BIOMASS (g AFDW · m⁻²)
20
15
10
5
0
0
74
93
100
HIGH
LOW
CHLOROPHYLL a (mg · m⁻²)
200
175
150
125
100
75
50
25
0
0
74
93
100
HIGH
LOW
SHADE (%)

Figure 3.1.

At 74 and 93% shade, this ratio was reduced to approximately 2, and no difference was observed in sections with 100% shade. In unshaded sections, combustible biomass was 12.8x higher in the low-density channel compared to the high-density channel. The difference was reduced to approximately 4.5 at 74 and 93% shade, and there was no difference at 100% shade. Mean biomass to chlorophyll a ratios varied from a high of 92:1 in unshaded sections of the low-density channel to a low of 23:1 in the 93% shade sections of the high-density channel.

During the fall, snail grazing increased diatom species richness, reduced cell density and enhanced the dominance of *Cocconeis* (Table 3.3). A comparison of tiles colonized for 40 days in the high vs. low-density channels, showed that snail grazing increased the number of diatom taxa from 11 to 16, decreased the number of algal cells by 34.6%, from 1078 to 705 per ml and shifted algal community composition towards adnate types of diatoms. The relative abundance of the adnate diatom, *Cocconeis placentula* var. *euglypta* was 91% in the high-density, but only 75% in the low-density channel. However, the relative abundance of the stalked and therefore more easily grazed diatom, *Gomphonema* sp. (probably *parvulum*) was 3x higher in the low-density channel compared to the high-density channel.

Snail Growth Rates

Mean monthly growth rates in both diversion channel populations reveal a distinct seasonal pattern (Table 3.2).

Table 3.3. Comparison of diatom species during the fall of 1985 in the high- and low-density snail populations in the diversion channel at Oak Creek, Benton County, Oregon.

Diatom Species	ABSOLUTE ABUNDANCE (%) Snail Density	
	HIGH	LOW
Cocconeis placentula var. *euglypta*	642(90.9)	809(74.8)
Gomphonema prob. *parvulum*	14 (1.9)	65 (5.7)
Acnanthes lanceolata	7 (1.4)	54 (5.1)
Other Species	42 (5.8)(1)	150(14.4)(2)
Total Number of Taxa	16(1)	11(2)
Cells·ml^{-1}(3)	705	1078

(1) Includes cf. *Acnanthes lanceolata*, *A. lanceolata* var. *dubia*, *A. lanceolata* var. *haynaldii*, *Fragilaria construens* cf. var. *pumila*, *Navicula cryptocephala*, cf. *Nitzschia dissipata*, *Rhoicosphaenia curvata*, *Synedra ulna*, and *S. ulna* var. *contracta*.

(2) Includes *Acnanthes minutissima*, *Nitzschia dissipata*, and *Synedra ulna*.

(3) The dilution factor was not recorded so it is not possible to determine density on a per unit area basis. Cell concentrations are meaningful only by comparison.

Growth was generally positive during the fall, spring and summer, and negative during the winter months. Marked individuals in the low-density population grew significantly faster than did those in the high density population during 6 out of 12 months. Mean growth rates declined in both populations during July and August of 1984, but the reason is not clear. Chlorophyll a standing crop was unusually low during July, 1984 (Table 3.2) which may account for the decline in growth that month, but growth was even lower in August in spite of an increase in chlorophyll a. During the winter, when both chlorophyll a concentrations and water temperatures were low, the snails were inactive (see dispersal section) and consequently feeding and growth were diminished.

Thus, both temperature and food availability were important in determining growth rates in the experimental channel. There was a highly significant correlation between mean monthly chlorophyll a standing crop and snail growth rate (Fig. 3.2). Temperature was the major limiting factor during the winter months for both populations. When temperature was high enough to allow growth (i.e. minimum temperature was above 4^{o}C and degree days accumulated monthly exceeded 130), food availability limited growth in the high-density population.

Growth rates of marked individuals were significantly higher for the low-density population than for the high-

Figure 3.2. Relationship between chlorophyll a standing crops and mean monthly growth rates of marked snails in the diversion channel at Oak Creek, Benton County, Oregon. Solid points are the high-density population and open circles are the low-density population. Spearman's rank correlation coefficient = r_s. The regression equation is y=0.021035x-1.27407.

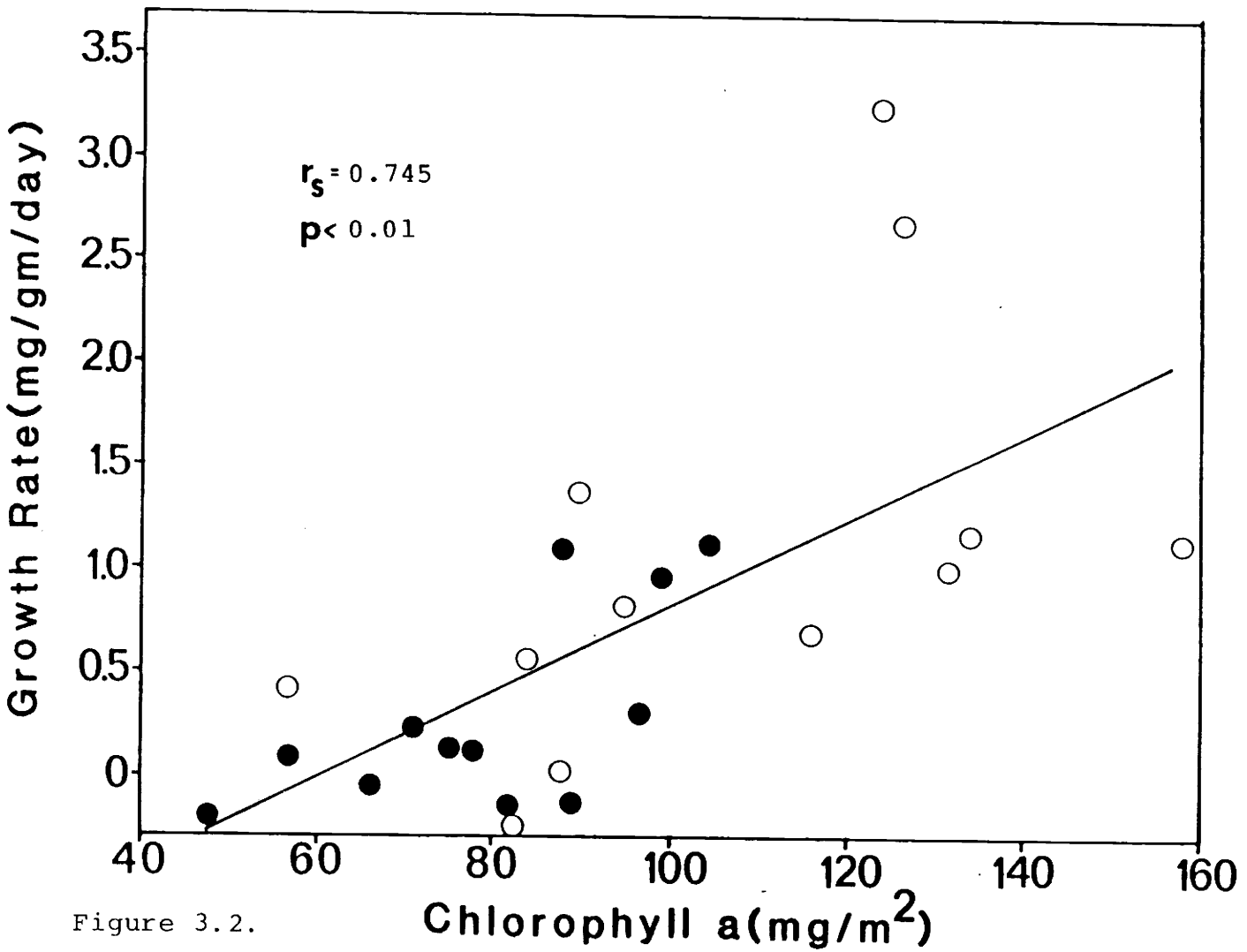

Growth Rate(mg/gm/day)
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0
$r_s = 0.745$
$p < 0.01$
40
60
80
100
120
140
160
Chlorophyll a(mg/m^2)

Figure 3.2.

density population on an annual basis (Fig. 3.3, ANCOVA for intercepts, $F_{1,43}=32.03$, $P<0.001$). The regression line fit to growth for the high-density population has an x-intercept at an initial fresh weight of 313 mg (or a shell length of 16.5 mm, calculated from equation 3.1) indicating that annual growth was zero for individuals of this size. For the low-density population the x-intercept occurs at 584 mg (shell length of 21.0 mm).

Growth rates from April to October of marked individuals released into Oak and Rock Creeks were similar to those of the low-density population in the experimental channel (Table 3.4). Sample sizes in the streams werebecause only 15% of the marked population was recovered compared to 30% for the diversion channel population. Mean growth rate in Oak Creek was 2.3 ± 0.4 $mg \cdot g^{-1} \cdot d^{-1}$ (n=14). In Rock Creek, growth rates of 2.5 ± 0.5 (n=17) and 5.4 ± 1.2 (n=7) were recorded for the riffle and pool populations, respectively. Mean growth rate in the pool was significantly higher than that in the riffle ($t=2.44$, $p<0.05$). Part of the reason that growth rates were higher in the natural streams compared to those in the high-density diversion channel was that the initial weights of individuals released into Oak Creek and Rock Creek were lower. For snails of comparable size, growth rates in Oak Creek were similar to those of the high-density diversion channel population, while growth rates in Rock Creek were

Figure 3.3. Relationship between initial body size and annual growth rates of marked individuals from the high- (solid points) and low-density (open circles) populations in the diversion channel at Oak Creek, Benton County, Oregon. Equations for the regression lines are b=3.112 and 4.116, and m=4.168 and 3.078 for the high and low density populations, respectively. The least squares regression lines fit to data for each population have significantly different elevations (ANCOVA, $F_{1,43}=32.03$, $P<0.001$).

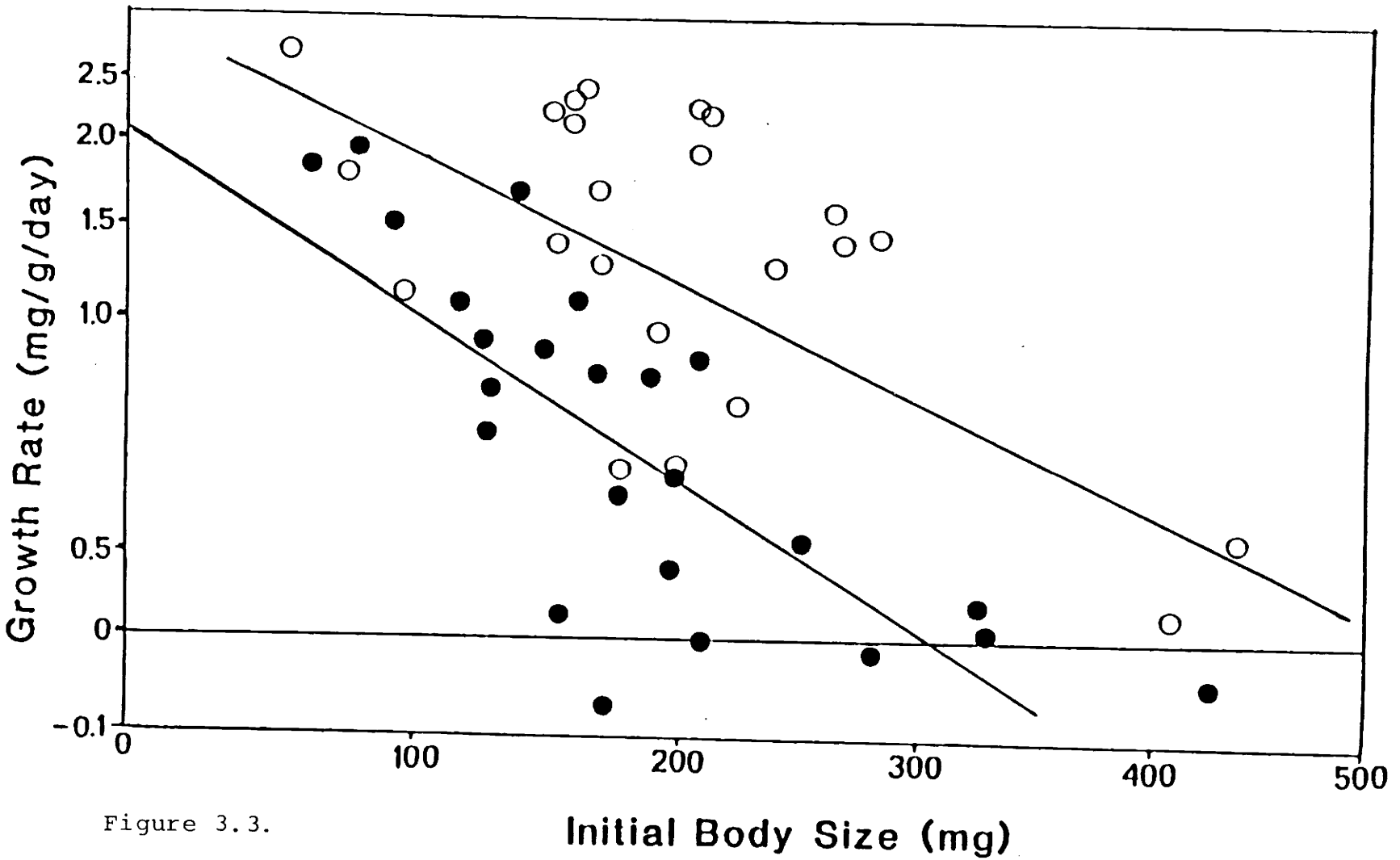

Growth Rate (mg/g/day)
2.5
2.0
1.5
1.0
0.5
0
-0.1
0
100
200
300
400
500
Initial Body Size (mg)

Figure 3.3.

TABLE 3.4. Mean rates of growth and dispersal ± 1 SE. of *Juga silicula* at two population densities in the high- and low-density populations in the diversion channel at Oak Creek, and in two populations in Oak Creek and Rock Creek, Benton County, Oregon. All records are based on mark-recapture methods.

POPULATION	N	MEAN INITIAL WEIGHT (mg)	GROWTH RATE ($mg \cdot g^{-1} \cdot day^{-1}$)	N	DISPERSAL ($cm \cdot day^{-1}$)	RHEOTAXIS: % MOVING UP	DOWN	ZERO[a]
DIVERSION CHANNEL								
HIGH DENSITY (83-84)	187	0.243	0.37 ± 0.10	275	48.8 ± 5.4	73	23	4
LOW DENSITY (83-84)	202	0.234	2.03 ± 0.18	294	29.3 ± 3.4	66	18	16
HIGH DENSITY (1985)	52	0.245	1.20 ± 0.21	73	140.5 ±12.3	97	3	0
LOW DENSITY (1985)	87	0.251	2.71 ± 0.19	49	99.4 ±11.9	98	0	2
OAK CREEK (1984)			Not measured	22	15.0 ± 2.3	50	50	0
OAK CREEK (1985)	14	0.142	2.3 ± 0.40	20	5.6 ± 1.2	60	40	0
ROCK CREEK (1985)								
RIFFLE	17	0.202	2.5 ± 0.53	48	11.1 ± 1.3	37	35	28
POOL	7	0.219	5.4 + 1.20	77	11.3 + 1.8	69	24	7

a Recorded as zero movement because no difference in position (upstream or downstream) was detected between release and recapture.

more similar to those in the low-density population.

Production

Annual production was 1529 $mg \cdot m^{-2}$ for the high-density population, compared to 1188 $mg \cdot m^{-2}$ for the low-density population (Table 3.5). Mean monthly standing crops for the high- and low-density populations were 13.3 and 2.1 $g \cdot m^{-2}$, respectively. These values yield P/B ratios of 0.115 for the high- and 0.566 for the low-density populations, nearly a five-fold difference.

The pattern of monthly production varied between populations. In the high-density population, 57% of the production occurred in June (Table 3.5). Production was also high in October, May and July. Three consecutive months with no production occurred from Januray to March. Production in the low-density population was less variable from month to month. It was highest in May, July, September and October. Growth during these four months accounted for 67% of total production in the low-density population.

The absence of growth and production for large snails in the high-density population and the low production recorded for the low-density population is due in part to degrowth during the winter and shell erosion. During the winter, when temperatures are low and snails are inactive, they must rely on protein tissue catabolism to sustain themselves and as a consequence individuals loose weight. Measurement of shell length for the diversion-channel

Table 3.5. Monthly production for five size classes of *Juga silicula* at two population densities from September 1983 through August 1984 in the diversion channel at Oak Creek, Benton County, Oregon.

MONTH	DEGREE DAYS (^{o}C)	SNAIL DENSITY	SHELL LENGTH (mm)					MONTHLY PRODUCTION ($mg \cdot m^{-2}$)
			0-5	5-10	10-15	15-20	20-25	
SEP	224	HIGH	55	148	185	-380	-101	-93
		LOW	55	49	98	-18	0	184
OCT	247	HIGH	3	11	39	52	2	107
		LOW	54	45	69	29	0	197
NOV	236	HIGH	19	57	79	-80	0	75
		LOW	24	9	15	4	0	52
DEC	129	HIGH	19	41	73	-65	-4	64
		LOW	7	2	1	-3	0	8
JAN	60	HIGH	-15	-31	-68	83	7	-24
		LOW	-2	-1	-2	0	0	-6
FEB	86	HIGH	-5	-10	-49	-41	-2	-106
		LOW	27	3	12	0	0	42
MAR	110	HIGH	-1	-4	-15	-12	0	-32
		LOW	6	3	12	14	0	35
APR	147	HIGH	5	14	57	37	2	115
		LOW	45	29	22	20	0	116
MAY	165	HIGH	42	84	167	1	0	295
		LOW	66	40	45	16	0	167
JUN	235	HIGH	75	210	545	48	0	877
		LOW	26	13	39	17	0	95
JUL	271	HIGH	49	97	111	-77	-4	175
		LOW	140	42	71	-1	0	252
AUG	253	HIGH	51	75	21	-65	-5	76
		LOW	11	5	21	8	0	46
TOTALS		HIGH	296	693	1143	-498	-105	1529
		LOW	459	240	403	86	0	1188

population revealed that the shells of some individuals with an initial length >15 mm were shorter after one year. The relationship between initial and final shell length over one year is defined by the equation:

$$SG = -0.64569\ (IL) + 9.3075,\ n=44,\ r^2=0.78 \qquad (3.6)$$

where SG=increase in shell length ($mm \cdot year^{-1}$) and IL=initial length (mm). Shell erosion was disproportionately high for the largest individuals in the population; smaller individuals rarely showed signs of erosion. Since weight changes were not partitioned between shell and tissue, the growth rates calculated for individuals >15 mm shell length must be considered as underestimates. Most of the snails in size classes IV and V were in the high-density population, so the underestimates of growth and production are higher for that population. However, snails with shell length >15 mm accounted for no more than about 9% of total production in either population, so shell erosion was of minor importance in the calculation of total production.

Although the mean density of 0+ year-class snails (i.e. shell length 0-5 mm) in the low-density population was 15% lower than that in the high-density population (low= $2034 \cdot m^{-2}$ vs. high= $2392 \cdot m^{-2}$, Table 3.1), annual production was 55% higher (low= 459 vs. high= 296 $mg \cdot m^{-2}$, Table 3.5). These observations, together with reduced growth rates, and differences in chlorophyll *a* concentrations, suggest that individuals in the high-

density population grew more slowly than those in the low-density population because of the effects of exploitative, intraspecific competition.

Dispersal

Mean rates of dispersal by marked individuals in the diversion channel populations varied with season and population density. The mean rate of dispersal in the high-density population was more than twice that of the low-density population during September and October 1983 (Fig. 3.4). Activity in the high-density population declined in November and there were no significant differences between populations during the winter months. Both populations averaged less than 15 $cm \cdot day^{-1}$ from December through March, and most individuals moved, or were displaced, downstream. The difference observed between populations in March was apparently due to chance and in any event it was not of great biological significance because dispersal was of minor consequence at that time. By April, snails in both populations were again active and mean dispersal exceeded 25 $cm \cdot day^{-1}$ for the remainder of the experiment. Dispersal was also significantly higher in the high-density population than in the low-density population during July and August.

Comparison of the dispersal histograms over the 12 months sampled (Fig. 3.5 a,b) shows that both populations had members that actively dispersed during the spring, summer and fall, but that the percentage of the population

Figure 3.4. Mean daily rates of dispersal for each month from September 1983 to August 1984 by marked snails in the high-(H) and low-(L) density populations in the Oak Creek diversion channel, Benton County, Oregon. Error bars represent ± 1 SE. Differences between means were assessed by Mann-Whitney U-tests. *=P<0.05, ***=P<0.001.

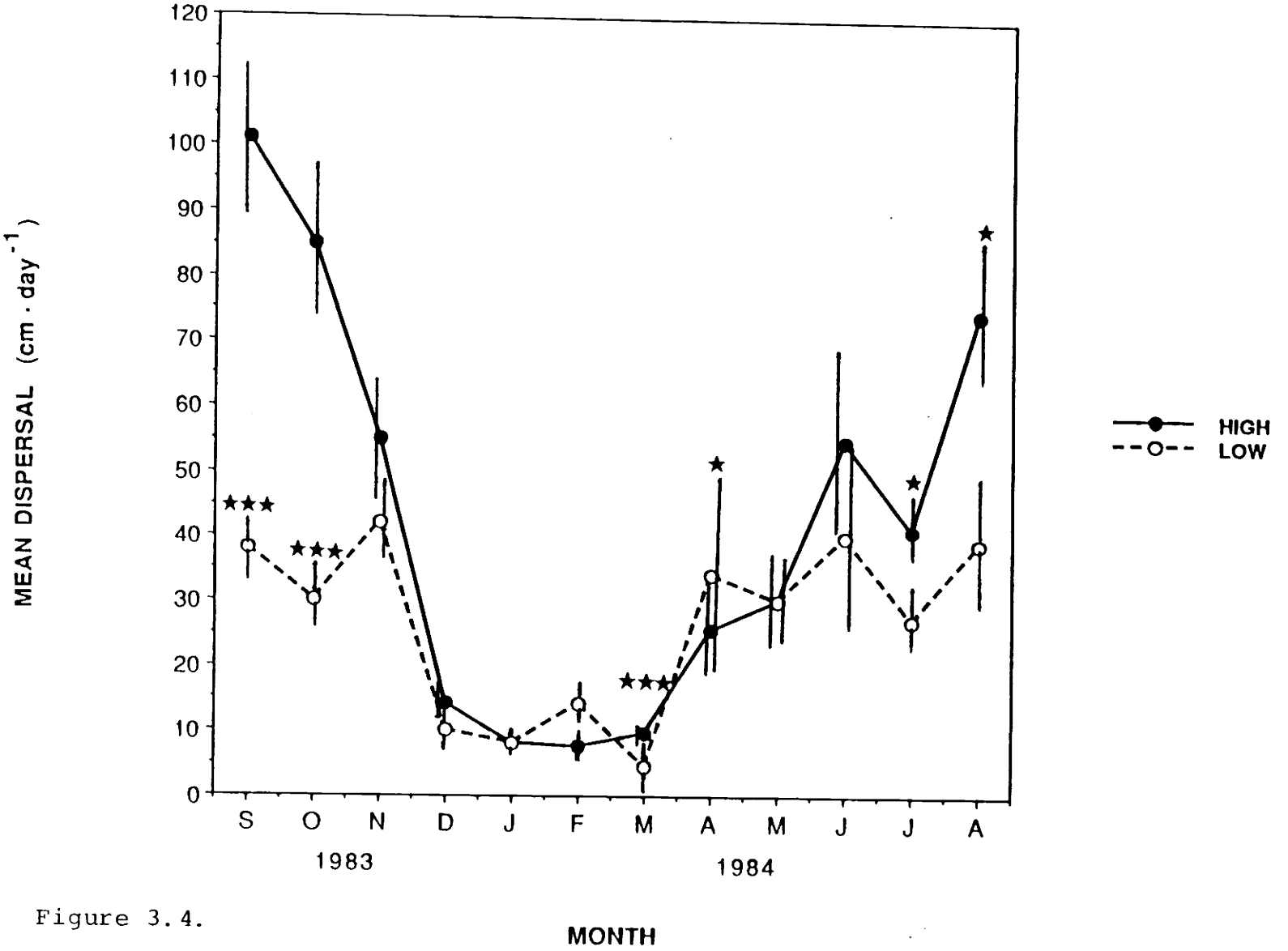
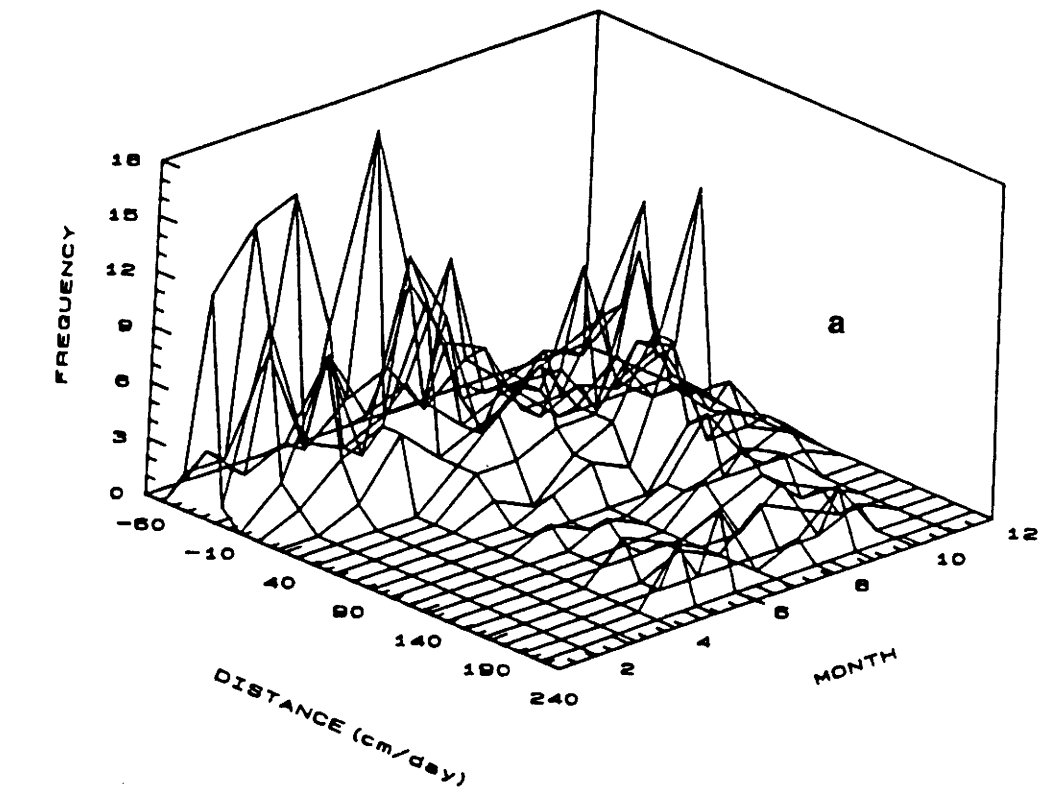

MEAN DISPERSAL (cm · day⁻¹)
120
110
100
90
80
70
60
50
40
30
20
10
0
S
O
N
D
J
F
M
A
M
J
J
A
1983
1984
MONTH
HIGH
LOW

Figure 3.4.

Figure 3.5. Rates of dispersal by marked individuals from the (a) high and (b) low density populations in the diversion channel at Oak Creek, Benton County, Oregon. Dispersal was monitored from September (month 9), 1983 through August (month 8), 1984.


FREQUENCY
18
15
12
9
6
3
0
a
-60
-10
40
90
140
190
240
DISTANCE (cm/day)
2
4
6
8
10
12
MONTH

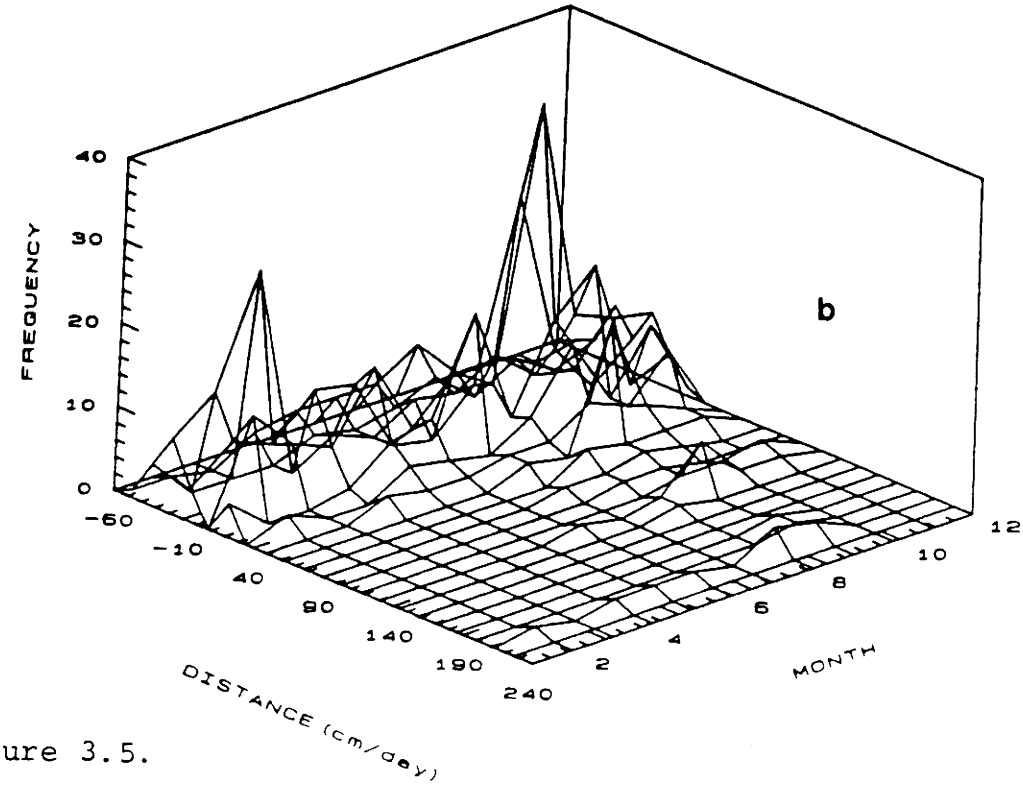

FREQUENCY
40
30
20
10
0
b
-60
-10
40
90
140
190
240
DISTANCE (cm/day)
2
4
6
8
10
12
MONTH

Figure 3.5.

actively dispersing was much higher for the high-density population. For example, in September, mean dispersal in the high-density population was 102 $cm \cdot day^{-1}$ vs. 38 for the low-density population, a highly significant difference. Of 128 observations in the low-density population, half of the snails moved <15 $cm \cdot day^{-1}$. Both populations also had individuals that moved in excess of 200 $cm \cdot day^{-1}$.

Rates of dispersal in the diversion channel were correlated with temperature and food availability. Linear regression of degree days accumulated vs. mean rate of dispersal for each month was highly significant (Spearman's rank correlation coefficient =0.79, $P<.001$, Fig. 3.6). The relationship between chlorophyll *a* and dispersal appears to be curvilinear: highest dispersal occurred at intermediate chlorophyll *a* concentrations (Fig. 3.7). Low temperatures during winter months resulted in low levels of chlorophyll *a* and dispersal. At chlorophyll *a* concentrations above about 100 $mg \cdot m^{-2}$ there was an inverse relationship between dispersal and chlorophyll *a*. These observations suggest that when food availability is high (i.e. in excess of 100 $mg \cdot m^{-2}$), snails can obtain enough food to sustain high growth rates by grazing in a localized area.

The relative abundance of snails congregating in the upstream gate area provides a general picture of seasonal variability in activity (Fig. 3.8). In general, upstream dispersal into the gate area of the diversion channel was

Figure 3.6. Relationship between monthly degree days accumulated (threshold temperature of 4°C) and mean rate of dispersal for the two diversion channel snail populations at Oak Creek, Benton County, Oregon from September 1983 to August 1984. Solid points represent means for the high-density population, and open circles represent means for the low-density population.

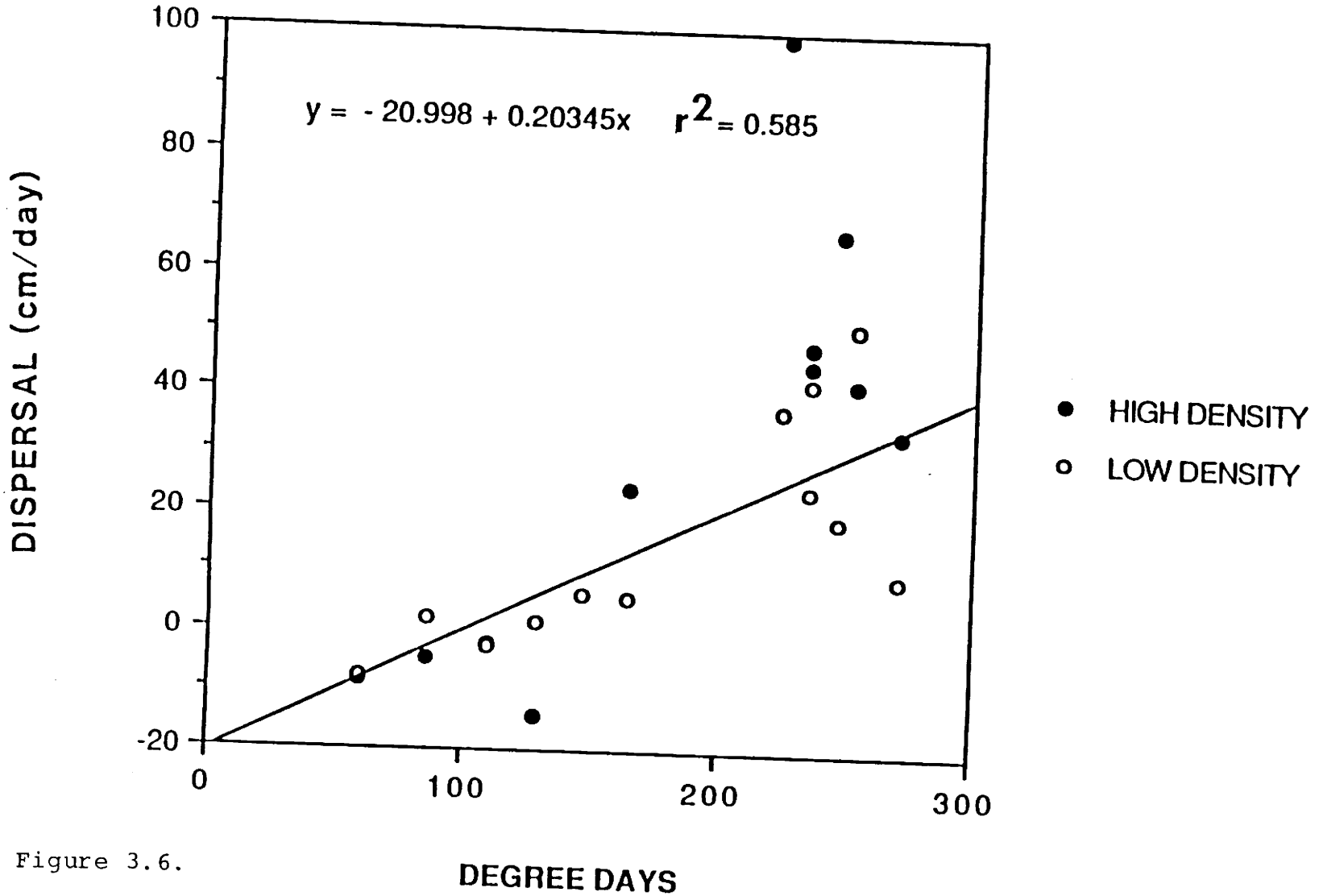

y = - 20.998 + 0.20345x
r2 = 0.585
DISPERSAL (cm/day)
100
80
60
40
20
0
-20
0
100
200
300
DEGREE DAYS
HIGH DENSITY
LOW DENSITY

Figure 3.6.

Figure 3.7. Mean monthly rates of dispersal by marked individuals vs. standing crop of chlorophyll *a* in the diversion channel at Oak Creek, Benton County, Oregon. Solid points are for the high-density population, and open circles are for the low-density population.

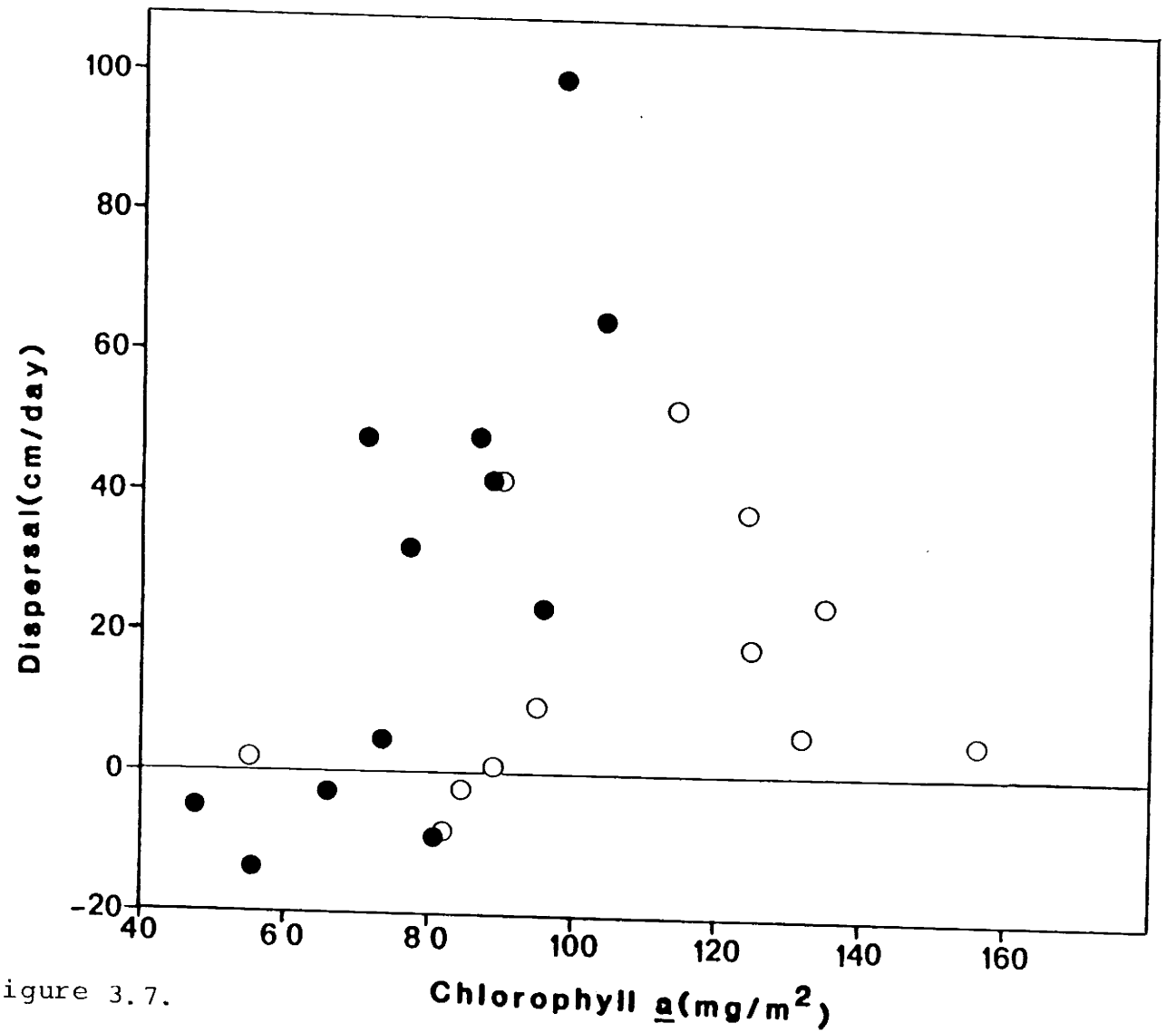

100
80
60
40
20
0
-20
Dispersal(cm/day)
40
60
80
100
120
140
160
Chlorophyll a(mg/m2)

Figure 3.7.

Figure 3.8. Estimate of the number of snails accumulating daily in the gate area (upstream end) of the diversion channel at Oak Creek, Benton County, Oregon from August 1983 to October 1985.

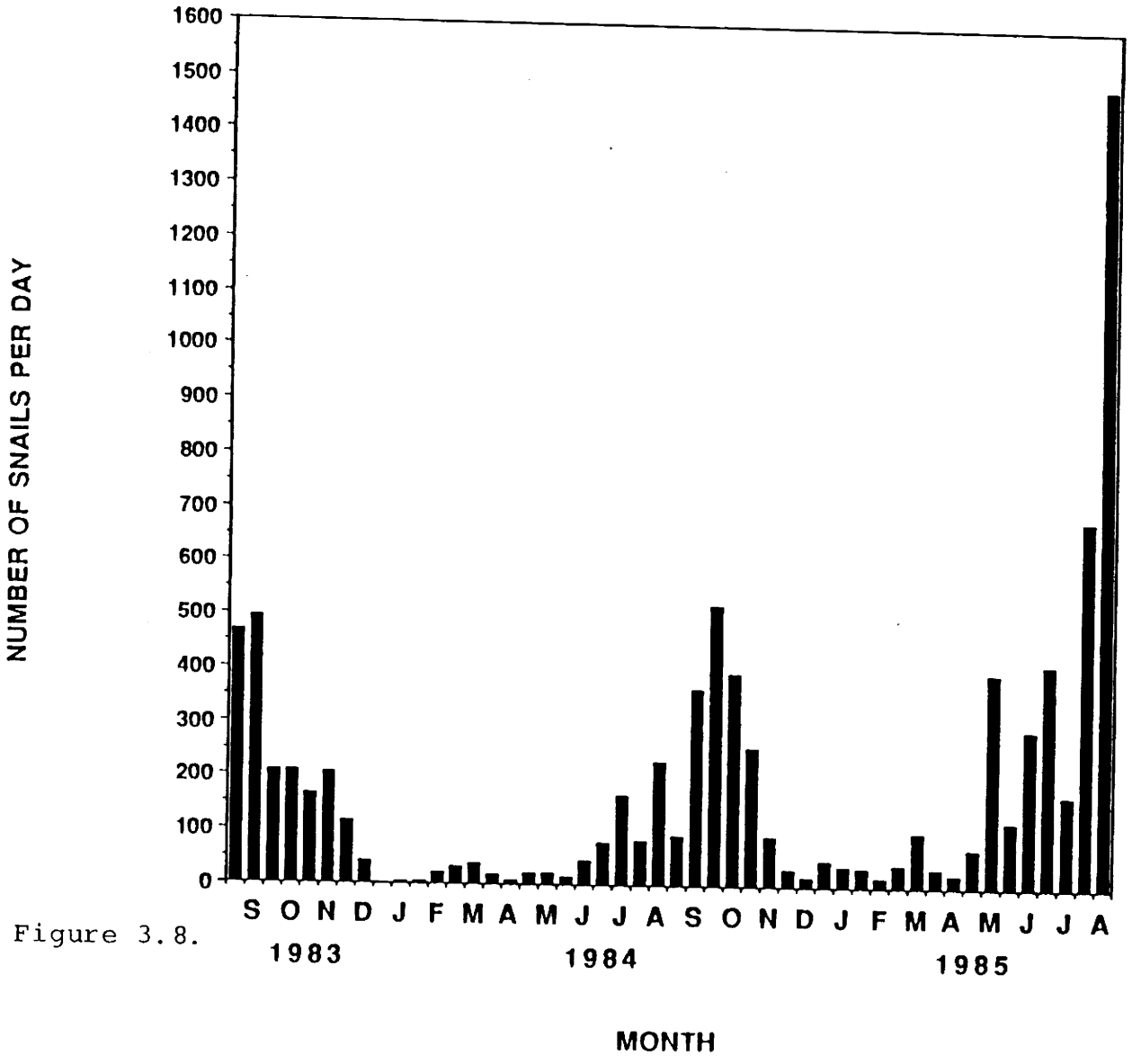

NUMBER OF SNAILS PER DAY
1600
1500
1400
1300
1200
1100
1000
900
800
700
600
500
400
300
200
100
0
S O N D J F M A M J J A S O N D J F M A M J J A
1983
1984
1985
MONTH

Figure 3.8.

high in the fall; this continued until December when the snails became quiescent. Dispersal was low during the winter and then increased again in the spring.

Undoubtedly some of the snails that made up this sample were deposited in the gate area from upstream, but there is good evidence that immigration from upstream did not contribute significantly to total biomass. Marked individuals were sometimes recaptured on the wrong side of the channel, and dispersal around and under the channel divider was the main source of snail immigrants in the low-density population. Relatively few snails were deposited in a net placed over the inflow during the fall. Also, the number of snails collected in the gate area was lowest during the winter when highest deposition of snails in the channel due to flooding would be expected.

Dispersal rates of snails in natural streams were lower, and positive rheotaxis less evident than in the experimental channel (Table 3.4). During the summer of 1984, the mean rate of movement was 15 $cm \cdot day^{-1}$ in Oak Creek compared with 49 $cm \cdot day^{-1}$ in the high-density population. Positive rheotaxis may have been less evident in Oak Creek because of irregularities in the bottom profile and current velocity, that resulted in frequent changes in orientation. Rheotaxis was less evident because snails were less restricted in choosing direction of movement (e.g. snails could disperse up to 200 cm across the stream compared to only 45 cm in the diversion

channel). The maximum distance travelled by any individual was 15 m upstream.

Although individuals released into the pool at Rock Creek grew significantly faster than those in the riffle ($t=2.44$, $P=0.023$), dispersal rates were indistinguishable (Mann-Whitney U-test, $p=0.14$). The maximum distance travelled by an individual over 80 days was 24.3 m upstream, which is equivalent to 30.4 $cm \cdot day^{-1}$.

Laboratory Studies

The laboratory population was sampled 18 times over 938 days to produce a growth curve for *J. silicula*. This amounted to an average sample of 20 individuals every 72 days. About 380 individuals (13% of the original population) were measured, dried and weighed. After nearly 1000 days, the stream was inadvertently drained, which killed most of the snails and the study was terminated. Out of an unsacrificed population of 2,620, 19% survived for 2 1/2 years. The last survivors were returned to Oak Creek in the spring of 1987, after over 1300 days or 3.5 years of growth. Average shell length was 16.4 mm, which was equivalent to approximately 300 mg fresh weight. Sexual maturity is apparent for snails with a shell length >13 mm and a wet weight >150 mg, and most lab-reared snails reached that size in about 3 years. Some individuals attained a sexually mature size after two years of growth in the lab but none was dissected to ascertain whether they were sexually mature.

For the first 370 days, a power curve model fit the growth data best (Fig. 3.9). The equation is:

$$TBDW = 0.00088\ (Days)^{1.67},\ r^2=0.97 \qquad (3.7),$$

where TBDW = total body dry weight.

A linear regression model fit the data well over the 1000 days (Fig. 3.9) and it is described by the equation:

$$TBDW = 0.06\ (Days) - 3.56\ ,\ r^2=0.96 \qquad (3.8).$$

The latter model is more parsimonious. There was however, an indication for the first 370 days of growth, that lab reared snails achieved exponential growth as described by equation 3.7.

The artificial streams provided good rearing conditions for *J. silicula*. Average shell length for the lab cohort at one year was 8 mm (4.16 mg total AFDW) vs. 3 mm shell length (0.20 mg) for both channel populations (Fig. 3.10). The maximum size attained by individuals in the diversion channel at one year was 5 mm (0.95 mg). After 3 years, the shells of the laboratory population were free of any signs of the shell erosion that is noticeable in field populations when individuals reach 15 mm shell length. Variability in individual size was very large. After nearly 3 years, mean shell length was 10.41 $\pm$ 1.56 mm (n=380), with a range from 7 to 16 mm.

In the 50-day study, growth was significantly affected by food quality. Analysis of covariance showed that carbon/nitrogen (C/N) ratio and % nitrogen had highly significant treatment effects on growth rate (Table 3.6).

Figure 3.9. Mean weight of a *Juga silicula* population maintained in a laboratory stream for about 3 years. The straight line is a linear regression calculated for 1000 days of growth, and the dotted line is a power curve calculated for the first 370 days.

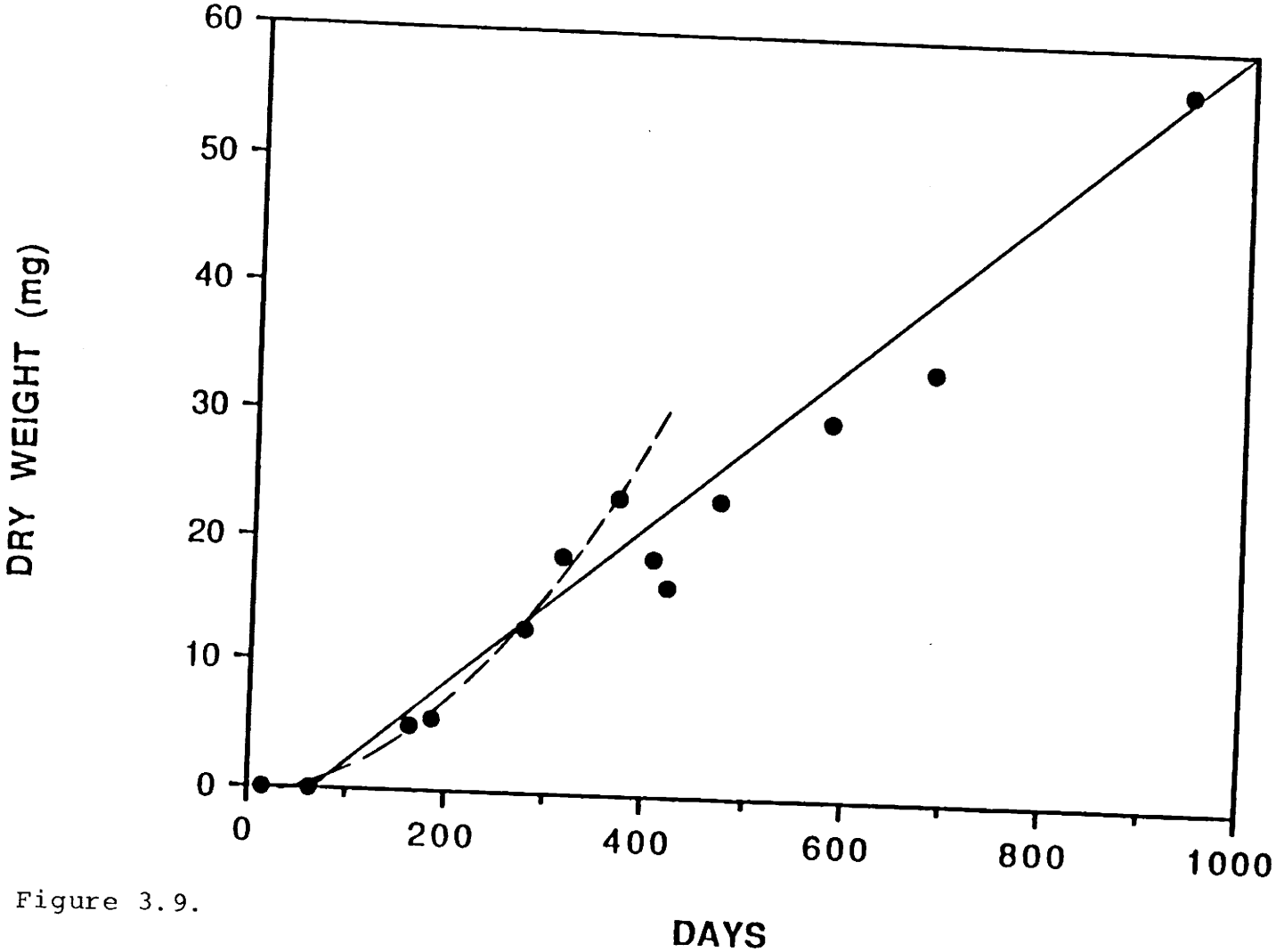


Figure 3.9.

Figure 3.10. A comparison of mean growth rates (measured as increase in shell length) for newly hatched snails in the Oak Creek Aquatic Laboratory stream and in the high- and low-density populations of the diversion channel at Oak Creek, Benton County, Oregon. The number of degree days accumulated in the channel populations was 2163 vs. 2225 for the laboratory population.

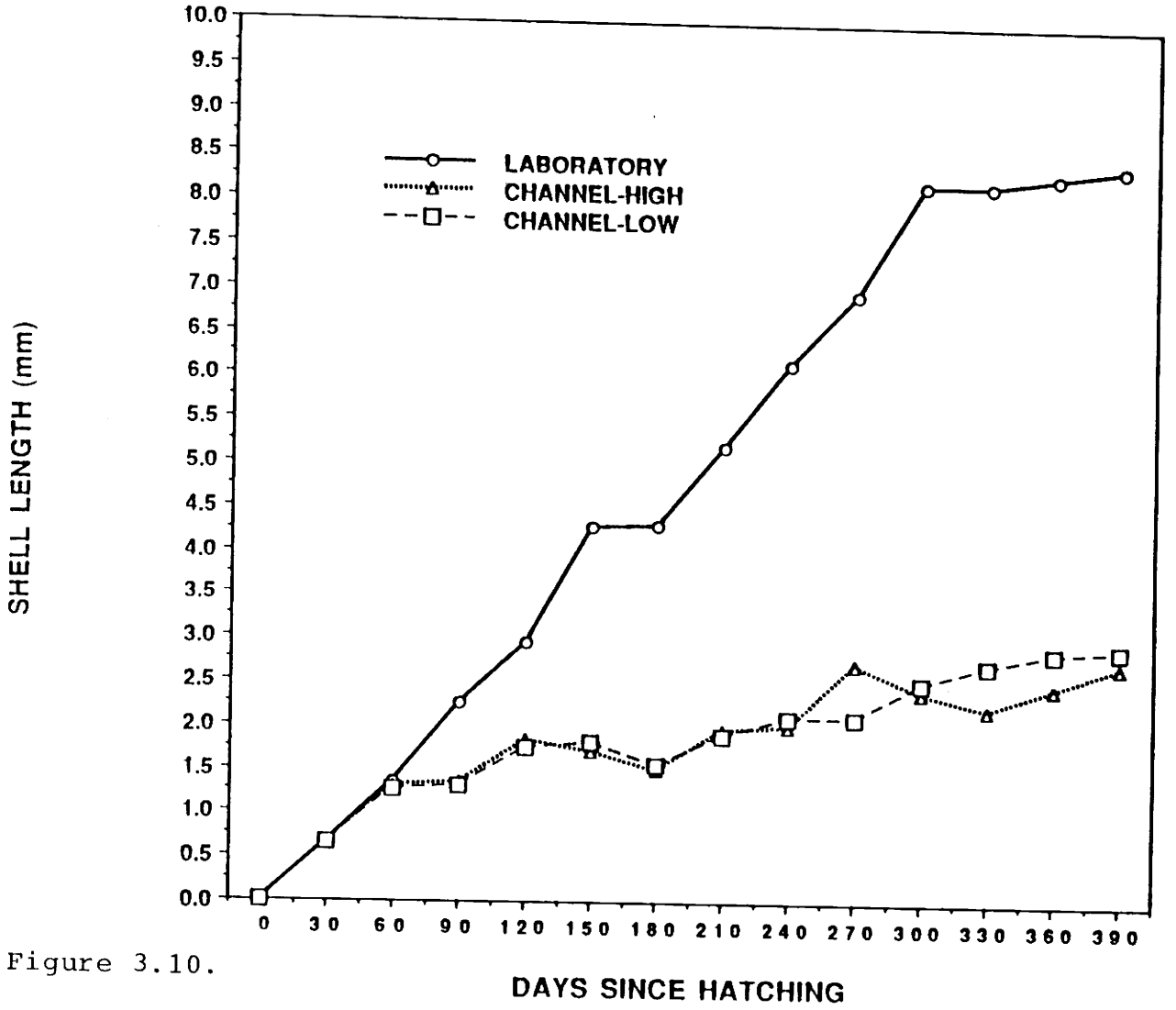

SHELL LENGTH (mm)
10.0
9.5
9.0
8.5
8.0
7.5
7.0
6.5
6.0
5.5
5.0
4.5
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
LABORATORY
CHANNEL-HIGH
CHANNEL-LOW
0 30 60 90 120 150 180 210 240 270 300 330 360 390
DAYS SINCE HATCHING

Figure 3.10.

Table 3.6. Results of ANCOVA assessing food quality treatment effects on growth rates of 2-year-old lab-reared snails in the Aquatic Laboratory at Oak Creek. ***=P<0.001

TREATMENT	d.f.	SUM OF SQUARES	MEAN SQUARE	F-RATIO	PROB.
Model	11	3.224	0.293	23.22	***
Covariates					
Carbon/Nitrogen	1	1.220	1.220	97.61	***
Initial Weight	1	0.908	0.908	71.91	***
% Nitrogen	1	0.245	0.245	19.45	***
Food Type	5	0.840	0.168	13.30	***
Block	3	0.012	0.004	0.31	ns
Error	106	1.346	0.012		
Total	117	4.562	0.039		

Food type also had a highly significant treatment effect. Snails grew best on periphyton, and on a combination of foods, with average rates of 12.50 and 10.89 $mg \cdot g^{-1} \cdot day^{-1}$, respectively (Table 3.7). Carrion ranked third at 9.45, followed by wood and unconditioned alder leaves at 8.04 and 7.99, respectively. Growth was poorest on FPOM at 4.15, but this rate was still significantly higher than the control group at 3.42. Food quality, defined by ranking growth rate from highest to lowest, did not change across the three size classes of snails used in the experiment (ANCOVA, NS); individuals in all size classes had highest growth rates on periphyton and lowest on FPOM.

Low growth rate on the FPOM-sand mixture is probably the result of poor food quality (high C/N ratio and low % N), as well as the snail's inability to ingest efficiently the fine, unconsolidated particles. The low, but positive growth recorded for the control group indicates that the snails were able to utilize food particles that settled in the trays from the water column. Snails were also commonly observed feeding on the undersurface of the mesh covering each tray where they may have been able to ingest food particles that accumulated there.

In the diversion channel, carbon:nitrogen ratios of periphyton ranged from 2.5:1 to 4:1 across shade treatments and showed no significant differences between populations during January of 1984. In August of 1984 however, C/N ratios were significantly higher in the low-density stream

Table 3.7. Growth rates of 2-year-old snails reared in the Oak Creek Laboratory on foods of different quality as measured by nitrogen content and carbon/nitrogen ratio (n=2 for each food). Values are means ± 1 SE. Differences between means were assessed by Student-Newman-Keuls multiple range tests. Growth rates with the same letter are not significantly different.

FOOD TYPE	QUANTITY OF FOOD PER WEEK (g AFDW)	% NITROGEN	C/N	N	GROWTH RATE (mg/g/day)	SIG.
PERIPHYTON	0.59	0.96±0.07	12.5±0.50	23	12.09±0.63	a
COMBINATION	1.05	--	--	22	10.89±0.50	ab
CARRION	0.12	7.94±0.34	7.2±0.10	24	9.45±0.65	bc
WOOD	0.61	0.84±0.26	63.5±20.36	24	8.04±0.48	c
ALDER LEAVES	0.11	2.25±0.09	21.6±1.06	23	7.99±0.64	c
FPOM	2.65	0.05±0.04	68.2±9.33	24	4.15±0.40	d
CONTROL	--	--	--	24	3.42+0.41	e

(11:1 vs. 7.5:1). These values are still well below the threshold ratio of 17:1 where food quality is reduced (McMahon et al. 1974), so differences in periphyton quality in the diversion channel do not appear to account for the observed differences in growth there.

DISCUSSION

Chlorophyll a Standing Crops

Actual periphyton abundance as standing crop biomass or net primary production was not measured in the Oak Creek study, but Gregory (1980, Fig. 19) demonstrated a well defined logarithmic relationship between chlorophyll *a* and periphyton gross primary production in laboratory streams. A standing crop of 150 mg chlorophyll *a* had a gross primary production of 0.6 mg $C \cdot m^{-2} \cdot day^{-1}$ compared to only 0.35 mg at a standing crop of 50 mg. Therefore, a threefold increase in chlorophyll *a* standing crop increased gross primary production by only 71%.

A good correlation between chlorophyll *a* and food abundance in the diversion channel was also evident during the spring of 1984 (Fig. 3.1). Chlorophyll *a* concentration and food abundance, measured as aufwuchs biomass were much higher for the low-density population compared to the high-density population.

Influence of Grazing by Snails on the Periphyton Community

Juga silicula appears to have selectively fed on *Gomphonema* and *Acnanthes lanceolata*. Although the channel that was heavily grazed by snails had a lower density of

periphyton, *Cocconeis placentula* var. *euglypta*, an adnate type, appears to have been less impacted than were the next two most common species. The lower ingestion rates of adnate diatoms by scrapers is a well established observation in laboratory streams (Sumner and McIntire 1982, Lamberti and Moore 1984), but is less commonly reported from natural streams. Douglas (1958) observed an inverse relationship between the density of *Acnanthes* sp. and the grazing caddisfly, *Agapetus fuscipes*. Patrick (1970) observed that the snail *Physa* did not feed effectively on either *Cocconeis placentula* or *Acnanthes lanceolata*, but for *J. silicula* this trend appears to hold true only for *Cocconeis*. Gregory (1980) reported that *Acnanthes lanceolata* came to dominate lab streams when *Juga* was excluded, whereas heavily grazed streams had a higher abundance of a smaller species, *Acnanthes minutissima*. In the channel at Oak Creek, *A. minutissima* was found only in the low-density channel, which is contrary to expectations.

There is some evidence that grazing by *J. silicula* increased species richness (Table 3.3). By reducing standing crops, snails may have reduced competition between algae and promoted their coexistence.

Snail Growth Rates

Comparison of growth rates in the two diversion channel populations shows that snail growth was highly dependent upon food availability (measured a chlorophyll a, Fig. 3.2). Grazing by the high-density snail population

decreased the abundance of algae during several months and food limitation, in turn, limited snail growth rate.

The relationship between food abundance and growth of *J. silicula* has been investigated in laboratory streams (Gregory 1983, Sumner and McIntire 1982), but the results are contradictory. Calculations based on data presented by Gregory (1983) show that mean laboratory growth rates (GwRt) are highly correlated with periphyton standing crop biomass (PB):

$$Gw\ Rt = 1.05\ (PB)^{0.597},\ n=4,\ r^2=0.98 \qquad (3.8)$$

and units for growth and biomass are mg wet weight$\cdot g^{-1}\cdot day^{-1}$ and g AFDW$\cdot m^{-2}$, respectively. In contrast, Sumner and McIntire (1982) found no consistent relationship between growth rates and periphyton biomass or gross primary production. Snails of similar sizes (8-11 mm shell length) were used in both studies, but Gregory (1980) had a maximum density much higher than that of Sumner and McIntire. His medium and low densities correspond to the range utilized by Sumner and McIntire (i.e. 1.5 to 8.8), which may in part explain the discrepancies between these two studies. Lamberti and Moore (1984) concluded, in their review of grazing in streams, that periphyton standing crop and production are most adversely affected when the resource is heavily grazed, a condition that appears to be the rule in most streams (Hart 1981, Lamberti and Resh 1983). Thus, a depression in snail growth would not be expected unless food resources were in limited supply due

to heavy grazing. These results are consistent with the interpretation that food resources limited snail growth.

Several field studies have demonstrated a correlation between food abundance and growth for freshwater snails (Eisenberg 1966, Cuker 1983, McMahon et al. 1974, Aldridge 1982) as well as the mayfly, *Ameletus validus* (Hill and Knight 1987). These results imply that some freshwater invertebrates are food limited at least during certain times of the year when physical constraints such as flooding are relaxed (Siegfreid and Knight 1977, Diamond 1982, Hemphill and Cooper 1983).

Food quality also has an important effect on growth rates of *J. silicula*. In the lab growth study C/N ratio best accounted for differences in growth rate (F-ratio =97.61, Table 3.6) compared to other measures of food quality. The high growth rate on periphyton is surprising considering that nitrogen comprised <1% of food weight. This finding supports the contention of McMahon et al. (1974) that C/N ratios are a good indicator of food quality. They proposed that foods having a ratio greater than 17:1 are not capable of supporting optimal growth because they do not contain sufficient protein.

Production

The production for J. silicula at Oak Creek was 1.5 $g \cdot m^{-2} \cdot y^{-1}$. This value is much lower than that of 11.7 $g \cdot m^{-2} \cdot y^{-1}$ calculated by Earnest (1967) for the Berry Creek population, but similar to values obtained for other

pleurocerid species. Richardson et al. (1988) used the instantaneous growth method to calculate production of two pleurocerid snails in a small Alabama stream. Both species are believed to have a life span of about 10 years. Annual production was 0.80 and 0.61 g AFDW·m^{-2} for *Elimia clara* and *E. cahawbensis*, respectively. Both species had a P/B ratio of 0.3 which is within the range of 0.19-0.58 calculated in this study. The Berry Creek population was probably atypical because of the controlled flow which prevented mortality from flooding (Diamond 1982) and the enriched conditions that increased food abundance and growth there. Variability in production from year to year may also have accounted for the difference between Oak and Berry Creeks.

Waters (1977) summarized production to biomass ratios for long-lived (i.e. >2 years) molluscs and concluded that the majority had values between 0 and 1, with maximal values of 5 in the tropics. He cautioned that production for a single species may vary widely between years. Species which live for 10 years or longer generally had much lower values, with P/B ratios ranging from 0.1 to 0.2. Considering that *J. silicula* has a life span of at least 3 years, the values calculated in this study agree well with predictions based on Waters' (1977) summary.

The observation that the majority of production by *Juga* occurs during a limited period of the year is not unexpected. Aldridge (1982) reported that growth of the

pleurocerid, *Leptoxis carinata*, was confined to two 3-month periods during its 25-month life cycle: the first three months of life (July through October) and May through August of the second year. Adult *Leptoxis* also had low or negative growth rates during the winter months when they lost 5-20% of their biomass. Like *J. silicula*, mortality was very high for the first few months of life. Survivorship was 5 to 20% of original egg mass densities after 4 months, but after 8 months life expectancy was high.

Dispersal

Dispersal behavior was influenced by both temperature and food availability. Temperature was the major limiting factor in the winter. During the summer, when temperature did not impede activity, dispersal was inversely correlated with food availability. Streit (1981) has shown that foraging behavior by the stream limpet, *Ancylus fluviatilus* is depressed at 2°C compared to 10°C and that periods of crawling without feeding are longer and more frequent if periphyton concentrations are too low. When food is patchily distributed, a consumer can enhance feeding success if it increases the rate of turning or decreases the rate of movement when it encounters a patch of high food concentration. This strategy has been adopted by many freshwater invertebrates (Bovbjerg 1965, Hart 1981, Wiley and Kohler 1984). In the diversion channel, there was some evidence of an inverse relationship between rate of

dispersal and chlorophyll *a* at concentrations above 100 $mg \cdot m^{-2}$ (Fig. 3.8).

The positive relationship between growth rate and chlorophyll *a* (Fig. 3.2) also may be an indirect measure of the cost of foraging in a stream where food resources are limited. Calow (1974) has calculated that as much as 20% of energy assimilated by *A. fluviatilus* may be allocated to mucus production associated with movement. In this study, one major reason for the differences in growth rates between the two diversion channel populations is that the high-density population expended more energy in foraging for food but received less return for its effort and, as a result, had lower growth rates than did the low-density population.

The positive rheotaxis observed for *J. silicula* has been observed for other pleurocerid snails (Crutchfield 1966, Foin 1967, Houp 1970, Kreiger and Burbanck 1976, Mancini 1978). Positive rheotactic behavior is related to both feeding and active upstream dispersal. Although the chemoreceptive capacity of *J. silicula* has not been studied, scavenging behavior was commonly observed. Snails congregated and fed on carrion, and growth in the laboratory was fairly high on this food source. Upstream dispersal also may represent chemoreceptive orientation towards carrion or other food exudates.

Positive rheotaxis is also an important means of dispersal into new habitats. Wright (1932) described the

probable routes and rates of post-glacial dispersal into an Indiana river basin by *Goniobasis* and *Pleurocera*, and positive rheotaxis appears to be the mechanism. If *J. silicula* mates in the fall as do other pleurocerids (Dazo 1965), dispersal by females that occurs before the onset of winter may be an important mechanism for colonization of new habitats. The maximum distance travelled upstream by marked individuals over three summer months was 15 meters in Oak Creek and 21 meters in Rock Creek. At these rates, dispersal is a very slow process but significant movement by members of a population may be achieved over several years if individuals can successfully overwinter in the new habitats they occupy.

CONCLUSIONS

In this study it has been demonstrated that (a) growth and (b) production by *J. silicula* are inversely density-dependent, and (c) dispersal is directly density-dependent. Based on laboratory growth rates, snails should achieve highest growth and production in streams where periphyton is the major food source available. Growth rates were significantly depressed when temperatures were 5oC or lower which precludes occupation of these habitats by snails where growth during warm months may not be sufficient to overcome the deficit required to overwinter.

CHAPTER IV

IMPACT OF THE STREAM SNAIL, *Juga silicula* ON THE AVAILABILITY OF LEAF LITTER FOOD AND HABITAT

Abstract

The influence of the stream snail, *Juga silicula* on leaf litter-processing was examined by comparing weight loss and macroinvertebrate colonization of alder leaf packs over 120 days at two snail densities, one similar to that of a normal stream and the other reduced by almost 90 percent. Leaf-pack processing rate was nearly doubled in the high-density treatment (90% weight loss at 114 days vs. 191 days in the low-density treatment). Reduction of snail density resulted in an increased density and biomass of colonizing invertebrates (i.e. number or weight per pack).

Macroinvertebrate abundance peaked at 50 days with 420 per pack in the high-density population and 581 per pack in the low. Numerically, copepods and chironomid midges (mainly *Brillia retifinis* and *Corynoneura* sp.) were most abundant. Biomass per pack was highest at 50 days in both populations, and biomass per g pack was significantly higher in the low-density population than in the high-density population from 10 to 50 days.

Based on these experiments and annual collections of litterfall, it is estimated that the population of *J. silicula* was capable of processing 35% of allochthonous inputs to the stream. By accelerating the rate of leaf processing, this one species can significantly reduce the abundance of food and the duration of its availability as food for other shredders and as habitat.

Introduction

The snail, *Juga silicula* (Gould) is an abundant and dominant species in Pacific Northwest streams. A major factor in its success is that it feeds on a variety of foods ranging from algae to leaves, wood and carrion. The influence of the snail as a grazing herbivore has been extensively investigated in laboratory streams (Gregory 1980, 1983, Sumner and McIntire 1982, Lamberti et al. 1987, Steinman et al. 1987). These studies have shown that grazing by *J. silicula* shifts periphyton community composition to adnate morphotypes, decreases standing crop of periphyton and stimulates primary production.

In a field experiment, Hawkins and Furnish (1987) found that grazing by *J. silicula* reduced the standing crop of periphyton and altered the abundance and distribution of many stream insects apparently through a combination of exploitative and interference competition.

The impact of *J. silicula* on the availability of allochthonous material in streams has not been studied. Considering the importance of leaf detritus to stream organisms (Minshall 1967, Webster and Benfield 1986) and the abundance of snails in leaf debris (Anderson et al. 1978, Anderson and Sedell 1979), *J. silicula* was expected to play a major role in determining leaf processing rates. Elwood et al. (1981) have shown that a related pleurocerid snail, *Elimia* (formerly *Goniobasis*) *clavaeformis*, is an important grazer-shredder in eastern forested streams.

Laboratory stream studies by Mulholland et al. (1985) demonstrated that feeding by *E. clavaeformis* accelerates the loss rates of coarse particulate organic matter (CPOM) and elevates the concentration of seston.

The snail's influence on patterns of colonization by other invertebrates was also examined to determine if it altered the assemblage of aquatic insects that used leaf packs as habitat or as food; these values were determined by expressing colonization as number per pack and biomass per gram of leaf pack remaining, respectively. Expressing colonization on the basis of density per pack emphasizes leaf packs as habitat patches where macroinvertebrates occur without necessarily utilizing leaf tissue as a food source. Macroinvertebrates that feed on leaves should occur at densities proportional to the amount of the food resource (i.e. the leaf pack). The appropriate unit to use in expressing this relationship is biomass per leaf weight.

This study was designed to measure the impact of *J. silicula* on leaf litter weight loss. There were two major objectives: 1) to quantify the contribution of the snail to the processing of leaf litter and 2) to determine whether the snail was capable of modifying the composition and abundance in the patch-specific community (sensu Reice 1974) involved in leaf processing. We also describe the abundance and seasonal availability of litterfall species and estimate the amount of broadleaf litterfall that the population of snails is capable of processing.

Methods

The study site was located at Oak Creek in McDonald Forest 10 km northwest of Corvallis, Benton County, Oregon. Oak Creek is a third-order stream in the eastern foothills of the Coast Range. *J. silicula* is abundant in the stream; its mean density is about $1100 \cdot m^{-2}$, or 4 g (range 1-20) $AFDW \cdot m^{-2}$ (Diamond 1977, Gregory 1980).

Litterfall was measured by placing ten traps, each 0.5 m^2, in the riparian zone along Oak Creek. Litter that accumulated in the traps was removed monthly, or at shorter intervals, sorted into broadleaf and other categories, oven dried at 50°C, and weighed. It is assumed that litterfall in the riparian zone is similar to inputs to the creek, because the stream banks are lined with woody vegetation at the study site and there is a lack of lateral movement of litter into the stream because the flood plain is broad.

Preliminary data on leaf processing rates in Oak Creek were collected by placing 5 grams of naturally abscised red alder (*Alnus rubra*) or Garry oak (*Quercus garryana*) leaves in mesh bags during the fall and retrieving them after 42 days. For each species, 16 mesh bags with several 1-cm holes punched in them to allow entry of macroinvertebrates were used. Weight loss was determined gravimetrically for each leaf pack. Macroinvertebrates colonizing the packs were pooled and sorted to the family or genus level, and then oven dried and weighed to determine the biomass of each taxon.

A controlled experiment to measure the impact of snails on leaf processing was conducted in a diversion channel. The channel was used to manipulate snail densities and has been described by Hawkins and Furnish (1987). Briefly, the diversion channel was divided in half length-wise to create two experimental streams, each 36 m long and 45 cm wide. Gravel, 5 cm in dia., was added to both channels to a depth of 15 cm. Cross-dividers were placed every 1.5 m to create a stair-step gradient and to delineate 24 sections for sampling. Mean water depth was 20 cm and current velocities were generally maintained at 15 $cm \cdot sec^{-1}$ except during major flood events. Temperature was monitored twice each week using a maximum-minimum thermometer. The channel was also covered with four shading treatments (0, 74, 93 and 100%). Subsequent statistical analysis revealed that shade had no significant effect on snail densities in leaf packs, leaf processing rates or colonization by macroinvertebrates, so all shade treatments were combined for analysis.

Snail densities were manipulated by seeding one stream with snails to create a density comparable to that of the natural stream at Oak Creek (hereafter referred to as the high-density treatment) and removing snails from the other (low-density treatment) once or twice a week. During the four months of the experiment, the mean biomass of snails in the low-density treatment was only 12% of that in the high-density treatment (1.6 vs. 13.2 g $AFDW \cdot m^{-2}$).

On September 15, 240 leaf packs of red alder (mean unleached dry weight of 3.7 g) were added to each side of the channel. Each pack consisted of 10 leaves picked just prior to abscission, fastened together with a buttoneer and tethered to the median stream divider so that the packs rested on the bed of the channel. The biomass of litter added was 55 g $DW \cdot m^{-2}$. Any additional leaf litter that was blown or washed into the channel was removed.

Twenty-four leaf packs were removed at 10-day intervals for 3 months from each experimental stream (4 shade treatments x 6 replicates). The last leaf packs were removed in two sets of 12 (3 replicates) at 120 and 150 days, terminating the experiment on February 15. Leaf processing rates in each channel were compared using analysis of covariance with the covariate defined as the number of days that leaf packs were exposed in the stream.

Snails in each leaf pack were counted and returned to the channel except on day 10 when they were sacrificed for biomass determination. Dry weight was converted to AFDW (tissue + shell) by the formula:

$$\text{Total AFDW} = -0.018 + 0.28(\text{Total DW}),\ n=29,\ r^2=.96. \qquad (3.1)$$

Mean snail weight on day 10 was multiplied by the number per leaf pack to calculate snail biomass on all subsequent sample dates.

In the laboratory, the leaf packs were rinsed in water to remove macroinvertebrates and sediments. The packs were then oven-dried at 55°C and their weight loss was

determined gravimetrically by comparison with the original weight corrected for oven drying and leaching in the stream. Ash-free dry weight (AFDW) was determined by combustion of leaf packs (n=4) collected on each sample date. Mean ash-free dry weight (AFDW) decreased linearly from 93% of leaf dry weight on day 10 to 80% on day 120, as the percentage of refractory material in the leaf packs increased.

Macroinvertebrates colonizing the leaf packs were collected on days 10, 30, 50, 70 and 120. A 100 um sieve was held downstream to capture macroinvertebrates and debris displaced when a pack was lifted from the water. Packs were placed in individual zip-lock bags and kept on ice until they were returned to the laboratory for washing. Macroinvertebrates were preserved in 75% alcohol until they were identified. They were oven-dried at 55^{o}C and weighed to the nearest 0.001 mg using a Cahn Electrobalance. No correction was made for weight loss due to preservation. Chironomids and copepods were subsampled by dispersing the sample over a grid and counting 25% and 12.5%, respectively. Midges were identified to at least the generic level for 5 pairs of samples from each treatment. Macroinvertebrates were assigned to functional feeding group based on categories presented in Merritt and Cummins (1984) and personal observations of gut contents. Total number and biomass of macroinvertebrates in leaf packs from each snail population were compared using paired t-tests or

Wilcoxon Signed Ranks tests when data were not normally distributed or variances were not homogeneous.

Calculation of leaf processing rates was accomplished by least squares regression of days or degree-days vs. percent leaf weight remaining or log of percent leaf weight remaining. The processing rate coefficient, k, was calculated by fitting a negative exponential function to the data:

$$W_t = W_o\, e^{-kt},$$

where W_o = initial weight, Wt = weight remaining after t days or degree days, and k is the processing rate (Petersen and Cummins 1974). Weights were corrected for leaching and oven drying each of which amounted to 19%.

Leaf consumption rates were measured in the laboratory using feeding chambers described by Hanson et al. (1983). Snails were starved for 24 hours and then offered 3 leached alder leaf disks in aerated chambers for 72 hours at 12°C. Leaf disks were also added to a series of control chambers containing no snails to correct for leaching weight loss.

Results

Annual input of deciduous leaves to Oak Creek from 1980-1985 averaged 315 g DW·m^{-2} (Table 4.1). This was 48.7% of the total annual litterfall. About 90% of the litter fell between September and the end of December. At this site, Oregon ash (37%) and red alder (28%) together accounted for about two-thirds of the total broadleaf input.

Table 4.1. Mean annual inputs of leaf litter to the riparian zone at Oak Creek, Benton County, Oregon from 1980-1985. Values are means ± 1 SE.

SPECIES	MEAN ANNUAL LITTERFALL ($g\ DW \cdot m^{-2}$)
Oregon Ash (*Fraxinus latifolia*)	116.70 ± 6.69
Red Alder (*Alnus rubra*)	89.27 ± 8.37
Big-leaf Maple (*Acer macrophyllum*)	73.84 ± 7.35
Garry Oak (*Quercus garryana*)	27.32 ± 4.84
Other	8.32 ± 0.75
TOTAL BROADLEAF	315.47 ± 23.36
TOTAL LITTERFALL*	647.80 ± 70.99

*Includes wood, conifer needles, flowers, fruits, moss and lichens.

Alder leaf litter in Oak Creek had a higher rate of weight loss than did oak litter. After 42 days, alder had an average loss of 51% (k=0.017) compared to oak which lost an average of only 22% (k=0.006). *J. silicula* was the major macroinvertebrate on both leaf species (Table 4.2). In alder litter bags, snail densities were almost 17 per bag and snail biomass was 40.8 mg per g DW leaf or 95% of the total. In oak litter bags, average snail densities were 20 per pack and snail biomass was 16.0 mg per g DW leaf or 87.8% of the total. Numerically, *Paraleptophlebia* and chironomids were the other major macroinvertebrates present on both leaf species.

Leaf processing rate in the high-density treatment of the diversion channel was significantly higher than in the low-density treatment (k=0.020 vs. 0.012, ANCOVA, $p<.001$, Fig. 4.1). These rates translate to a 90% weight loss in 114 days in the high-density treatment vs. 191 in the low-density treatment. Percent weight losses were corrected for 48 hours leaching and oven drying, both of which amounted to 19%. Mean AFDW decreased linearly from 93% of DW on day 10 to 80% on day 120. Leaf processing in the high-density treatment fit the negative exponential model well ($r^2=0.98$). However, linear regression provided the best fit for processing in the low-density treatment ($r^2=0.95$ vs. 0.79 for the negative exponential model). Fitting the data to an exponential model using degree days

Table 4.2. Densities (number per bag) and biomass (mg per bag) of macroinvertebrates colonizing mesh bags containing an initial weight of 5 g of red alder or garry oak leaves in Oak Creek, Benton County, Oregon after 42 days in the Fall (October to November). At the end of the experiment, mean weights for alder and oak litter were 2.45 (51% weight loss) and 3.90 (22%) g DW, respectively.

Functional Feeding Group	Red Alder		Garry Oak	
	Density	Biomass	Density	Biomass
Shredders	23.1	103.10	32.7	65.94
Juga silicula	16.9	100.00	20.3	62.38
Lepidostoma	0.8	0.57	0.9	0.61
Nemouridae	0.6	0.25	0.8	0.13
Paraleptophlebia	4.5	2.00	9.1	2.19
Other	0.3	0.28	1.6	0.63
Collectors	4.6	0.42	5.5	0.56
Ptychoptera	0.4	0.36	0.3	0.29
Chironomidae	4.1	0.02	4.7	0.16
Other	0.1	0.04	0.5	0.11
Grazers				
Heptageniidae	0.2	0.05	0.1	0.05
Predators	1.6	1.67	2.9	4.49
Rhyacophila	0.3	0.11	0.5	0.14
Octogomphus specularis	0.2	0.98	0.1	1.16
Predaceous Plecoptera*	1.1	0.58	2.2	1.63
TOTAL	29.5	105.24	41.2	71.04

* Perlidae and Perlodidae

Figure 4.1. Weight loss curves for alder leaf packs placed in the high- and the low-snail density treatments in the diversion channel at Oak Creek, Benton County, Oregon from September 15, 1983 to February 15, 1984. $k=0.020$ for the high density treatment and 0.012 for the low density treatment. The slopes of the lines are significantly different (ANCOVA, $P<0.001$).

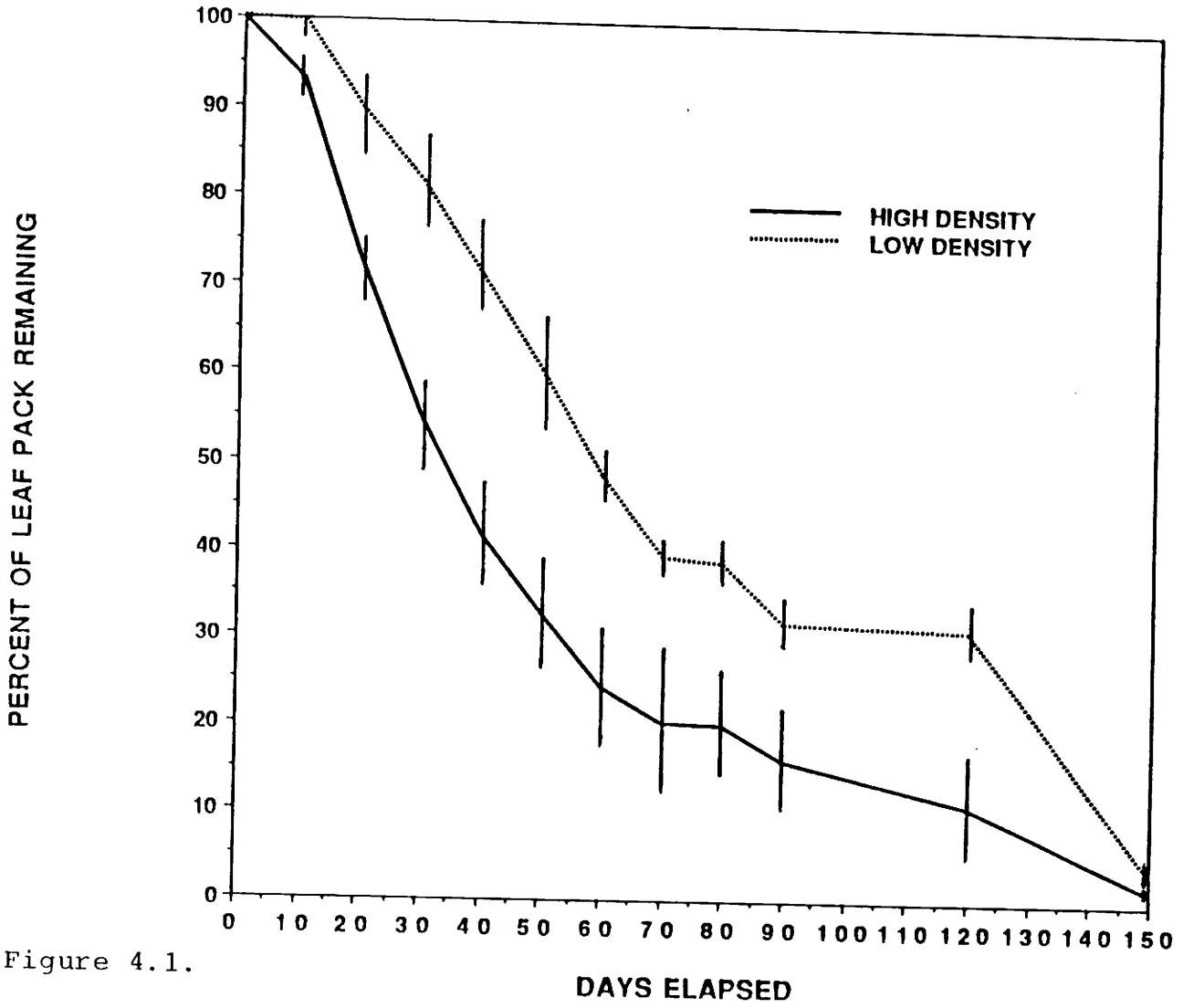

PERCENT OF LEAF PACK REMAINING
100
90
80
70
60
50
40
30
20
10
0
HIGH DENSITY
LOW DENSITY
0 10 20 30 40 50 60 70 80 90 100 110 120 130 140 150
DAYS ELAPSED

Figure 4.1.

rather than days consistently produced a fit that was either no better (r^2=0.96 for high-density packs) or worse (r^2=0.71 for low-density packs).

At 10 and 20 days, the leaf packs in the high-density treatment averaged about 14 snails per pack. From 30-40 days, snails averaged less than 10 per pack and from 50 days to the end of the experiment average abundance never exceeded 5. In the low-density treatment, the average number of snails per pack was >1 only on day 10. Snail biomass per pack declined rapidly from >300 mg at 10 and 20 days, to <50 mg from 70 days until the end of the experiment (Fig. 4.2). In contrast, snail biomass·per g pack was more variable from one sample to the next, but overall it declined gradually from 100-150 mg during the first 60 days to <50 thereafter (Fig. 4.2). Thus, snail biomass per pack tracked the rapid weight loss of leaves and snail biomass·per g pack declined only gradually for at least the first 60 days. These findings indicate that snails utilized the packs in proportion to the amount of food the packs provided.

Macroinvertebrate density per pack increased rapidly up to 30 days (Fig. 4.3). By day 50, densities had reached a maximum in the high-density treatment, regardless of whether copepods were included or not. In contrast, numbers continued to increase in the low-density treatment up to day 50 when maximum densities were reached.

Figure 4.2. Biomass of *J. silicula* in alder leaf packs in the high- and low-density treatments from September 15, 1983 to January 15, 1984 in the diversion channel at Oak Creek, Benton County, Oregon. Data are expressed as weight (mg AFDW) per pack and weight per gm pack.

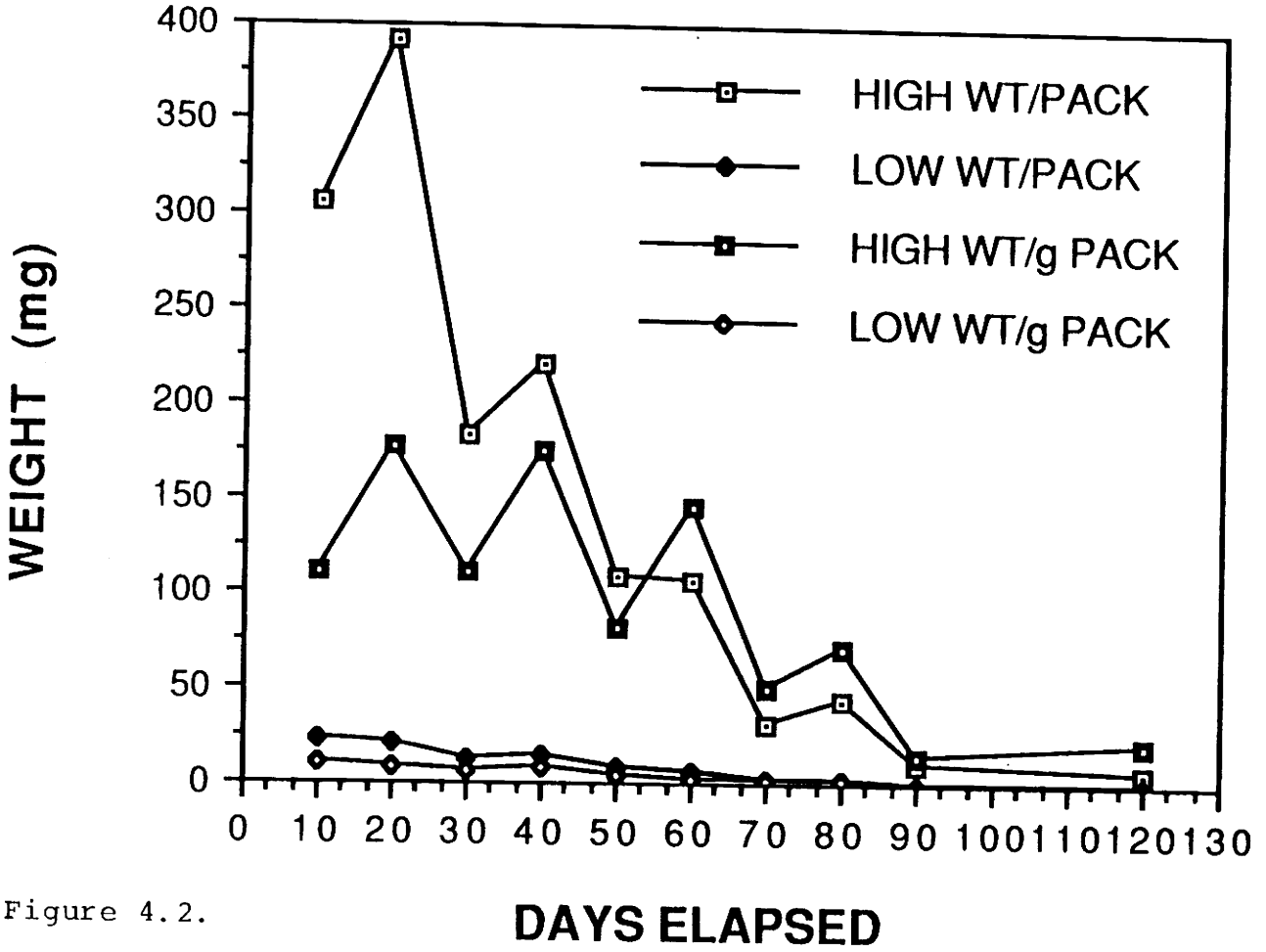

400
350
300
250
200
150
100
50
0
WEIGHT (mg)
HIGH WT/PACK
LOW WT/PACK
HIGH WT/g PACK
LOW WT/g PACK
0 10 20 30 40 50 60 70 80 90 100110120130
DAYS ELAPSED

Figure 4.2.

Figure 4.3. A comparison of the number of macroinvertebrates colonizing leaf packs from the high-and the low-density treatments in the diversion channel at Oak Creek, Benton County, Oregon. Data are expressed as abundance (number per pack) including and excluding copepods. Statistical comparisons were made using paired t-tests.

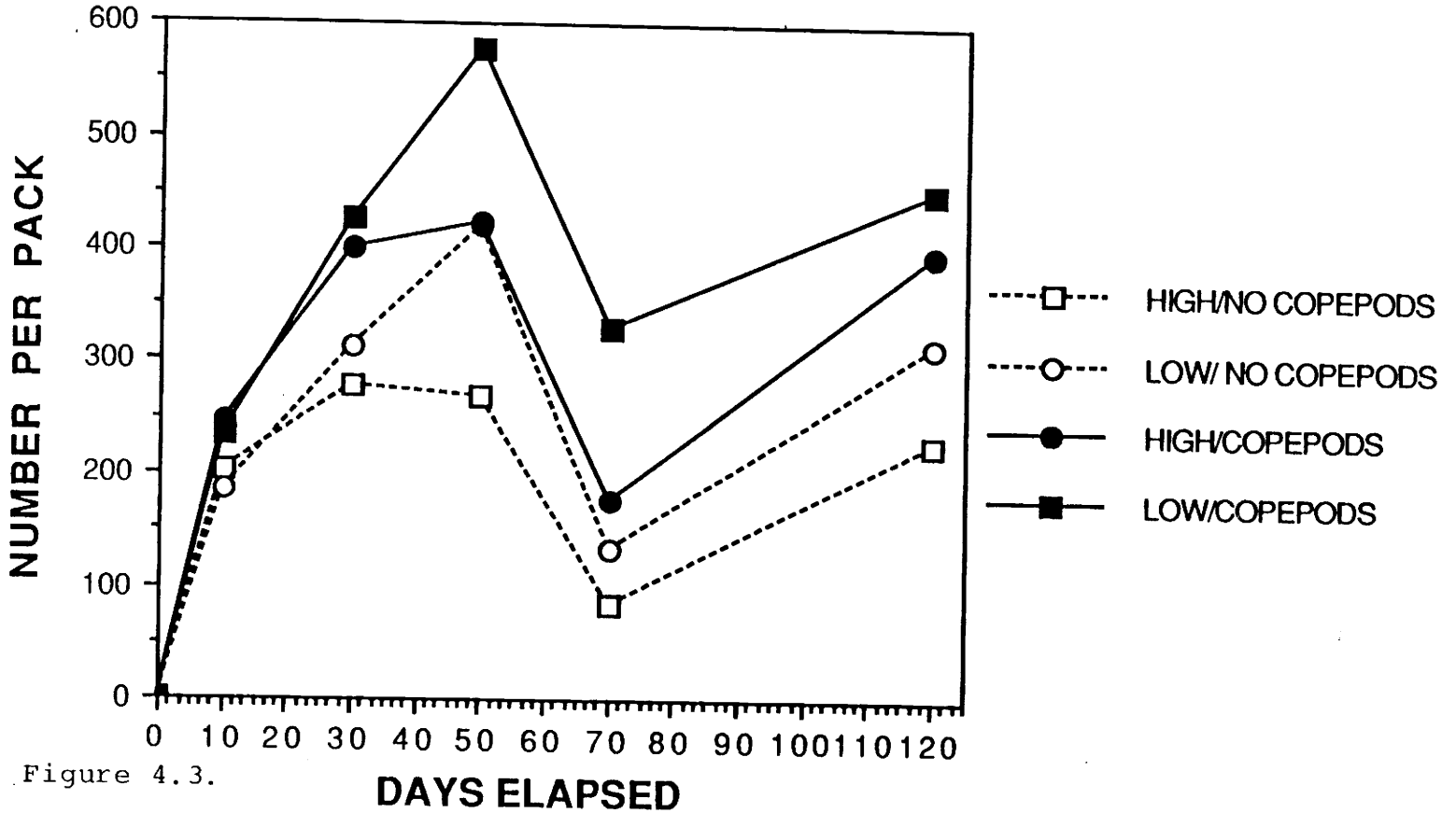

NUMBER PER PACK
600
500
400
300
200
100
0
0 10 20 30 40 50 60 70 80 90 100110120
DAYS ELAPSED
HIGH/NO COPEPODS
LOW/ NO COPEPODS
HIGH/COPEPODS
LOW/COPEPODS

Figure 4.3.

In both treatments, mean number declined at 70 days and increased again at 120 days.

Total macroinvertebrate densities were consistently higher in the low-density treatment packs (Fig. 4.3), but the differences on any given day could not be distinguished statistically (t-test, NS). Total chironomid densities were not significantly different on any days.

When colonization is expressed as biomass per g leaf pack, snails were always the major macroinvertebrate colonizing the packs, but their relative abundance rapidly decreased as the weight of leaf packs decreased (Table 4.3). In the high-density treatment, snails exceeded 100 mg per g pack on day 10 which was 98% of the total biomass. By day 50, snails had declined to 81.6 mg per g pack, (94% of macroinvertebrate biomass) and by day 120, they were only 16.5 mg per g pack, but this was still 81% of the mean total biomass. Even though snail biomass was reduced by 91% in low-density treatment packs, snails still made up a major portion of the total biomass. However, its relative abundance steadily decreased from 75% at 10 days to 35% at 50 days and 0% at 120 days. Total biomass per g pack for all other macroinvertebrates combined was significantly higher in the low-density treatment packs for the first 50 days of the experiment (Table 4.3). Biomass was greatest at 50 days in both populations. Although total biomass per g pack was significantly higher when snails were removed, there was no difference between the high- and low-density

Table 4.3. Comparison of dry weight biomass (mg per g pack) of functional groups and major taxa in alder leaf packs for selected sample days in the high- and low-density treatments at Oak Creek, Benton County, Oregon. N=24 for each treatment, except on day 120 when N=12. Differences between treatments were determined by Wilcoxon's signed-ranks and Mann-Whitney U tests (120 days only). (*=P<0.05, **=P<0.01, ***=p<0.001)

DAYS LEAF PACKS EXPOSED		10	30	50	70	120
MEAN PERCENTAGE	HIGH	93.1	55.1	45.0	20.7	11.0
OF PACK REMAINING	LOW	99.7	81.7	72.4	49.5	32.9
SHREDDERS(excluding	HIGH	1.00	3.06	2.66*	0.64**	0.39
Juga)	LOW	1.39	3.96	4.31	1.44	1.17
Juga silicula	HIGH	109.86***	111.20***	81.63***	31.46***	16.53***
	LOW	9.40	6.40	3.60	2.20	0.00
Paraleptophlebia	HIGH	0.54	0.48	0.32	0.16	0.10*
	LOW	0.81	0.74	0.41	0.11	0.27
Malenka	HIGH	0.26	0.84	0.35**	0.11*	0.06
	LOW	0.39	0.69	1.36	0.33	0.13
Capniidae	HIGH	0.05	0.08**	0.00	0.00	0.00
	LOW	0.05	0.28	0.00	0.00	0.00
Pteronarcella	HIGH	0.06	0.36	0.28	0.00	0.00
	LOW	0.04	0.20	0.49	0.00	0.00
Lepidostoma	HIGH	0.05	0.20	0.41	0.13	0.02
	LOW	0.06	0.33	0.23	0.18	0.01
Brillia retifinis	HIGH	0.04	1.10**	1.27	0.21***	0.02
	LOW	0.04	1.72	1.82	0.80	0.00
COLLECTORS	HIGH	0.26	0.29	0.46	0.22	0.31
	LOW	0.30	0.32	0.44	0.34	0.44
Corynoneura	HIGH	0.12	0.07	0.02	0.02	0.03*
	LOW	0.13	0.11	0.02	0.01	0.12
Rheocricotopus	HIGH	0.02***	0.04	0.22	0.03	0.02
	LOW	0.05	0.08	0.26	0.05	0.04
Copepods	HIGH	0.12	0.07	0.02	0.02**	0.03
	LOW	0.13	0.11	0.02	0.01	0.12
SCRAPERS	HIGH	0.41	0.60	0.07	0.22***	0.17*
	LOW	0.61	0.60	0.27	0.35	0.33
Baetis	HIGH	0.28*	0.50	0.05	0.19***	0.05
	LOW	0.34	0.38	0.22	0.18	0.23
Epeorus	HIGH	0.13	0.11	0.02	0.03*	0.12*
	LOW	0.27	0.22	0.05	0.17	0.10
PREDATORS	HIGH	0.41	0.55	1.32	2.07	2.94
	LOW	0.77	1.58	1.58	2.84	2.26
Perlidae	HIGH	0.38	0.40*	1.06**	1.48	2.54
	LOW	0.71	0.94	1.32	2.62	1.93
Perlodidae/	HIGH	0.02	0.15	0.26	0.59	0.40*
Chloroperlidae	LOW	0.06	0.64	0.26	0.21	0.33
TOTAL MACROINVER-	HIGH	111.93***	115.68***	86.12***	34.61***	20.33***
TEBRATE BIOMASS	LOW	12.46	12.86	10.20	7.17	4.20
BIOMASS EXCLUDING	HIGH	2.08*	4.50**	4.50**	3.15	3.81
SNAILS	LOW	3.06	6.46	6.61	4.97	4.20

treatments for any functional feeding group for the first 30 days of the experiment. Shredders reached a higher biomass than any other functional group for the first 50 days of the experiment. On days 70 and 120 predators were most abundant.

The total biomass per pack of non-snail macroinvertebrates peaked at 50 days in both treatments, but reached a significantly higher value in the low-density packs (19.77 vs. 11.06 mg per leaf pack, Fig. 4.4). Removing snails from the stream allowed the biomass of macroinvertebrates to reach a higher level at 50 days compared to the high-density treatment where the biomass per pack remained relatively unchanged from 30 to 50 days. Most of the increase in biomass in the low-density treatment between days 30 and 50 was by predators. In the low-density treatment, the colonization trajectory continued to increase up to 50 days. Total biomass, and biomass of scrapers and shredders was significantly higher in the low-density treatment on day 70.

On a taxon-specific level, a shift is apparent in the species of shredders occupying the leaf packs (Table 4.3). In contrast to *Paraleptophlebia* and *Malenka* which colonized rapidly and persisted at relatively high densities for the duration of the experiment, other shredder taxa reached peak densities at discrete time periods. For example, *Pteronarcella* and *Lepidostoma* (*quercina* and *unicolor*) reached highest densities midway through the processing

Figure 4.4. A comparison of the biomass per leaf pack of different functional groups from the high- and the low-snail density treatments over 120 days in the diversion channel at Oak Creek, Benton County, Oregon. For each stacked bar pair, the bar on the left is for the high- (H) density treatment packs and the right is for the low (L).

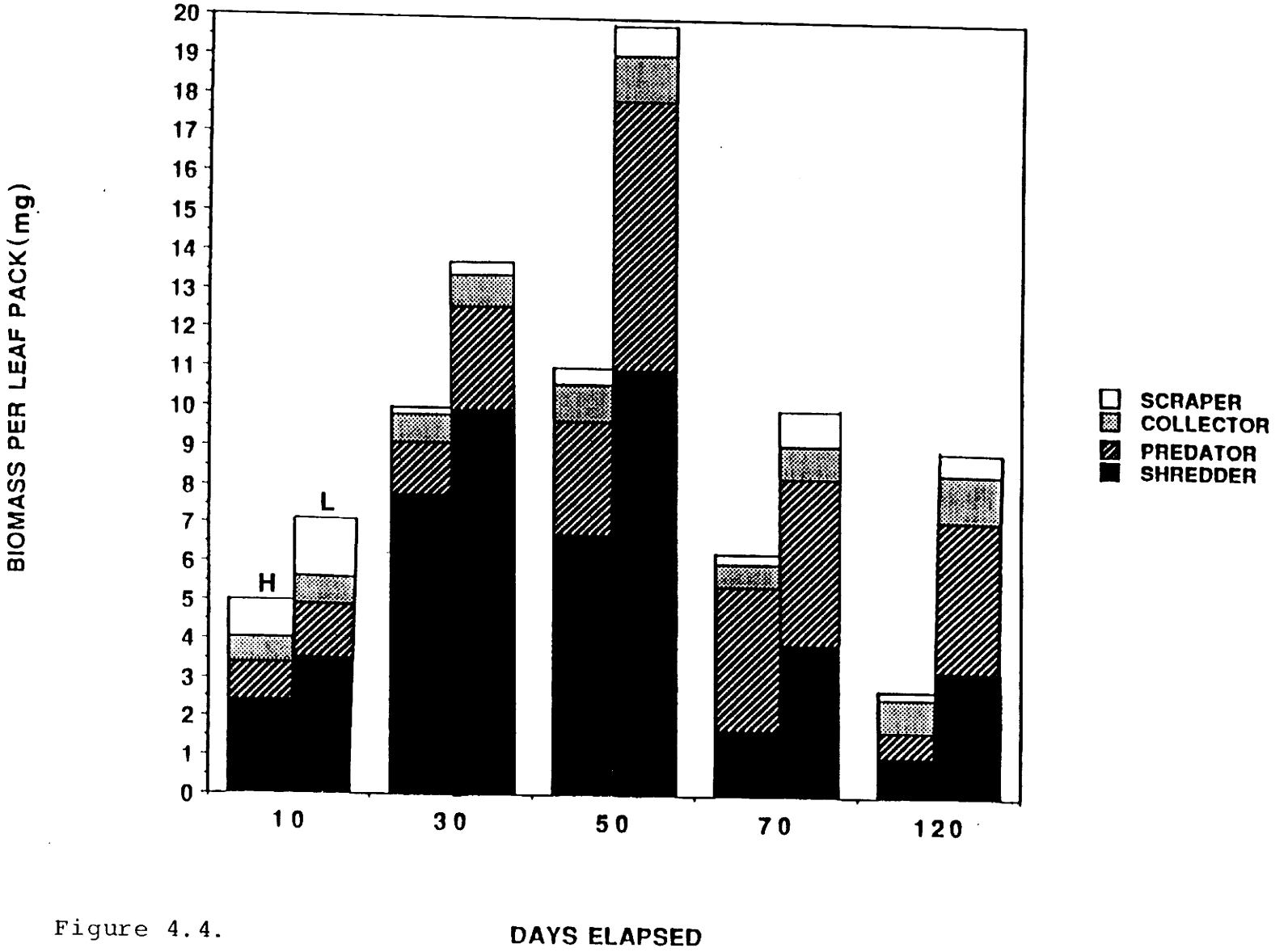

BIOMASS PER LEAF PACK(mg)
20
19
18
17
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
0
H
L
10
30
50
70
120
DAYS ELAPSED
SCRAPER
COLLECTOR
PREDATOR
SHREDDER

Figure 4.4.

sequence (e.g. 30 to 50 days). Anderson and Grafius (1975) found that leached but unconditioned red alder leaves were readily consumed by *Lepidostoma quercina*, but palatability increased with conditioning time. The reasons for *Lepidostoma*'s late appearance in the leaf packs is probably related to leaf palatability as well as its life cycle which is timed to exploit deciduous leaf litter inputs (Anderson 1976).

Another shredder, *Brillia retifinis* also reached peak biomass at 50 days. Its abundance declined afterwards and the reason for this is best explained by its life history. A generation of B. *retifinis* appears to have emerged from the stream after the first 50 days (i.e. mid-November). Evidence for a major emergence of *Brillia* include: 1) the occurrence of pupae in leaf packs at 50 days; 2) a decline in densities of *Brillia* from 587 to 201$\cdot m^{-2}$ in benthic samples taken on days 60 and 90; and 3) a shift in the mean dry weight of individuals in leaf packs from 0.232 mg on day 50 to 0.079 mg on day 70.

Corynoneura also emerged from the stream around day 70 as evidenced by declining densities in leaf packs and the benthos, and a smaller mean size of individuals on day 120. A second generation recolonized the packs at 120 days which in part explains why *Corynoneura*'s biomass increased on the final sample day.

Discussion

These results provide experimental evidence that a single member of the macroinvertebrate community had a major influence on the availability of an important food resource in streams. *J. silicula* consistently altered the density and biomass of macroinvertebrates per pack, and accelerated the disappearance of leaf debris from the stream. Whereas leaves were 90% processed in 114 days in the high-density treatment, processing in the low-density treatment was prolonged to at least 190 days, which extended the availability of leaf litter as both food and habitat.

This study also strengthens the evidence that macroinvertebrates play a major role in processing allochthonous material in forested streams (Cummins et al. 1973, Wallace et al. 1982, Benfield and Webster 1985, Mulholland et al. 1985, Barnes et al. 1986). Assuming that snails, which were present at a density of 122.6 $mg \cdot g^{-1}$ leaf and comprised 98.4% of the biomass were responsible for an equal percentage of the processing that occurred, allows us to calculate a consumption rate of 150.8 mg $leaf \cdot g^{-1}$ $snail \cdot day^{-1}$ (18.79 mg leaf x 0.984/0.1226 g $snail \cdot day^{-1}$).

If snails are present in the stream at a density of 5 $g \cdot m^{-2}$, they are capable of processing 754 mg $leaf \cdot day^{-1}$. From the litterfall data, annual leaf litter inputs were about 300 g $DW \cdot m^{-2}$, 88% of which falls from September through December. Thus about 2 g $AFDW \cdot day^{-1}$ is delivered to the stream during this fall period mostly as Oregon ash and

red alder. Since ash and alder have similar, fast processing rates (k>0.01, Petersen and Cummins 1974), and together comprised about 2/3 of total broadleaf inputs, *J. silicula* was capable of processing daily 754 mg of the 2 gm entering the stream, which was 35% of the total.

J. silicula did not behave like a typical shredder, because it colonized leaves as soon as they were available rather than waiting until they become conditioned by microorganisms. In this sense, *Juga* behaves like the caddis larva *Potamophylax cingulatus* L. which was observed by Otto (1974) to prefer green over withered alder (*A. glutinosa*) leaves.

Another shredder which appears to prefer fresh, green over autumn-shed leaves is the chironomid midge, *Brillia flavifrons*. Stout and Taft (1985) found that *B. flavifrons* was the principal shredder of tag alder (*A. rugosa*) in two Michigan streams where it was observed to grow better on fresh alder leaves than on autumn shed leaves. *Brillia retifinis* was a major shredder in the Oak Creek channel where it reached highest densities at 50 days suggesting that its life history may be adapted to take advantage of a high availability of conditioned leaves rather than fresh ones. In spite of the high densities of *B. retifinis* in benthic samples during September when fresh leaves were introduced to the stream, significant numbers of *Brillia* were not observed in leaf packs for another month.

Macroinvertebrate biomass per pack excluding snails

peaked at 50 days in both channels. These results are consistent with the interpretation that palatability is optimal for shredders after a period of conditioning by hyphomycete fungi and bacteria (Kaushik and Hynes 1971, Mackay and Kalff 1973, Iversen 1974, Bärlocher 1980, Golladay et al. 1983). Triska et al. (1975) found that fall microbial processing of red alder, as measured by respiration, was maximal at 78 days in Mack Creek and Watershed 10. Microbial respiration and macroinvertebrate biomass may peak sooner in Oak Creek than in the Cascade Range streams because Oak Creek is warmer.

Decomposition rates in Oak Creek vary considerably between summer and fall. Anderson and Sedell (1979) observed that in midsummer at about 15°C, red alder leaves placed in mesh bags were completely skeletonized in less than one month. They concluded that although fungi conditioned the leaf, tissue loss was primarily due to rasping by snails, leptophlebiid mayflies and nemourid stoneflies. Both temperature and invertebrates were important contributors to leaf processing.

The processing rates observed in this study for the low density packs are comparable to the rates measured for streams in the Cascades where snails are absent or rare. Sedell et al. (1975) measured processing coefficients of 0.0124 in Watershed 10 (1st order, no snails) and 0.0168 in Mack Creek (3rd order, snails very rare) during the fall season. Both of these streams are located in the Cascade

Mountains at elevations of 700-1400 meters. The elevation at the Oak Creek site is 150 meters and water temperatures are warmer. These values translate to 50% processing in 70-90 days vs. 60 days in the low-density treatment channel at Oak Creek. In the high-density treatment only 40 days were required to reach 50% weight loss, which is comparable to rates observed in Oak Creek, where snails are abundant and 50% loss was achieved in 41 days in mesh bags. Part of the explanation for the slower processing rates in the Cascade streams may be the lower temperatures there. Gregory (1980) reported that mean temperatures in Mack Creek during the fall declined from a mean of 9°C in September to 5°C in November. During this same period in Oak Creek, temperatures declined from 14 to 10°C.

The decomposition rates for alder observed in Oak Creek during the fall were generally lower than those reported for other geographic regions. Short and Ward (1980) described decomposition of *Alnus tenuifolia* in two Rocky Mountain streams from September to December and concluded that rates were temperature dependent with 50% weight loss reached at 15-30 days and faster processing above 10°C. Short and Ward (1980) calculated mean biomass of macroinvertebrates to be about 14-42 mg/g leaf pack with higher biomass associated with faster processing. Shredder biomass never exceeded 2 mg per g leaf so they concluded that temperature was more important than macroinvertebrates in determining weight loss. Hart and Howmiller (1975) observed that processing of

Alnus rhombifolia was complete in only 34 days in a coastal stream in California where temperatures ranged from 10-12°C. These faster rates were achieved even though macroinvertebrate densities were lower than for Oak Creek. Biomass peaked at 25 days with a value of 460 mg wet weight (WW) per g dry weight leaf (or 76.7 mg DW based on a conversion factor of 0.167 DW/WW, Waters 1977). Assuming that the composition of these alder leaf species is similar compels us to conclude that shredder biomass is not necessarily a good predictor of processing rates.

In contrast to the above trend, *J. silicula* did not behave like a typical shredder because no period of conditioning was necessary in order for it to feed extensively on leaves.

CONCLUSIONS

Shredding activity by *J. silicula* is of major importance in determining the availability of leaf litter as a food source and a habitat in streams. Its feeding activity nearly doubled the rate of alder leaf weight loss and caused a depression in the abundance of macroinvertebrates utilizing alder leaf litter as a food source and habitat. It did not, however behave like a typical shredder because it preferred unconditioned leaves.

CHAPTER V

SYNTHESIS: *Juga silicula* IN STREAM ECOSYSTEMS

A major theme that has emerged from studies of stream ecosystems during the past 20 years is the interrelationship between physical and biotic factors, but the relative importance of each in structuring communities is still a matter of debate (Minshall and Petersen 1985, Power et al. 1988). Variation in the physical environment, due mainly to the uneven distribution of habitat patches (Pringle et al. 1988, Townsend 1989), and disturbance regimes (Resh et al. 1988) affects biotic interactions that ultimately are expressed in community structure and function. Stream organisms respond to the physical environment by concentrating in areas that best provide the necessary resources for growth and reproduction. They also must respond to the biotic environment by adjusting their distribution to take advantage of food-rich patches, avoid predators and react to the organisms that overlap with them in resource use when the resource is in limited supply.

There is considerable evidence that stochastic disturbances, such as flooding, exert a major influence on community structure commensurate with their frequency and intensity (Hynes 1970, Siegfried and Knight 1977, Fisher

et al. 1982, Resh et al. 1988). Disturbance may also maintain nonequilibrium conditions by preventing populations of macroinvertebrates from growing to a size where density-dependent controls begin to operate when the carrying capacity of the environment is approached (Hemphill and Cooper 1983).

Competition is the biotic factor that has received the most attention as a primary variable determining stream community structure (Patrick 1975, Wiley 1981, Schoener 1983, Hart 1984, McAuliffe 1984). However, Minshall and Petersen (1985) recognized that documenting the existence of competition does not prove its importance in structuring communities. They attempted to reconcile the apparent conflict between those who espouse a belief in the greater importance of either physical or biotic factors by pointing out that each is valid depending on circumstances. Either stochastic, non-equilibrium or deterministic, equilibrium mechanisms might best account for community structure depending upon successional stage in a colonization sequence. During the initial phase in the colonization of a habitat patch, macroinvertebrate density is far below carrying capacity and increases exponentially; therefore, biotic interactions are of little importance initially. As the habitat fills to carrying capacity, density and species richness become asymptotic, and competitive interactions begin to operate. The salient feature in predicting the importance of

competition is the successional stage of the community. Clearly an understanding of the interplay between physical and biotic variables is necessary to understand and predict the complex distribution patterns in streams.

Paine (1966, 1980) developed a compelling argument for the importance of identifying keystone species or strong interactors in food webs as a useful means of interpreting and understanding the complexity of communities. A consumer is a strong interactor if pronounced changes occur when it is removed from the community. If such dominant species exist in stream ecosystems, then attempts to understand how biotic interactions structure communities can be simplified by concentrating attention on those species. In this context, *J. silicula* was chosen as a subject for study because it appeared to be a good candidate for a strong interactor. It is often very abundant, constituting greater than 50% of the community biomass, and it is a food generalist so its influence was expected to be pervasive and broad scale. Hawkins and Furnish (1987) presented evidence that the intensity of competition between *J. silicula* and other macroinvertebrates varies with shade and substrate particle size. They concluded that attempts to specify the capacity of snails to influence community structure must await more precise study of its distribution and seasonal activity.

This dissertation addresses some of these questions

and also quantifies the impact that *J. silicula* has on the availability of autochthonous and allochthonous derived foods. A conceptual framework showing the factors considered in this dissertation is presented in Fig. 5.1. According to this scheme, variation in the physical environment, geographically and temporally, affects an array of biological features such as abundance, distribution, competition, production and mortality. This constellation of biological factors in turn determines the capacity of the snail to influence production by autotrophs, the availability of allochthonous food and habitat, and the distribution and abundance of other macroinvertebrates through competition. Associated with each variable are references to published studies. I have attempted to understand how variation in the physical variables of temperature, light, substrate and current velocity interact to determine food availability, and growth, production and dispersal behavior by *J. silicula*. Specifically, I have examined seasonal growth and dispersal at two population densities, quantified the impact of *J. silicula* on the availability of autochthonous and allochthonous foods, and attempted to define its microhabitat preferences. Each of these studies will be summarized separately, and then related to one another in order to show how they may interact to determine the intensity of competition by *J. silicula*.

Figure 5.1. The hierarchy of factors affecting the distribution and abundance of Juga silicula. Literature that pertains to a particular subject is given in parentheses below the category to which it applies. Stars indicate aspects that were studied in this thesis.

Hierarchy of factors affecting the abundance & distribution of *Juga silicula*

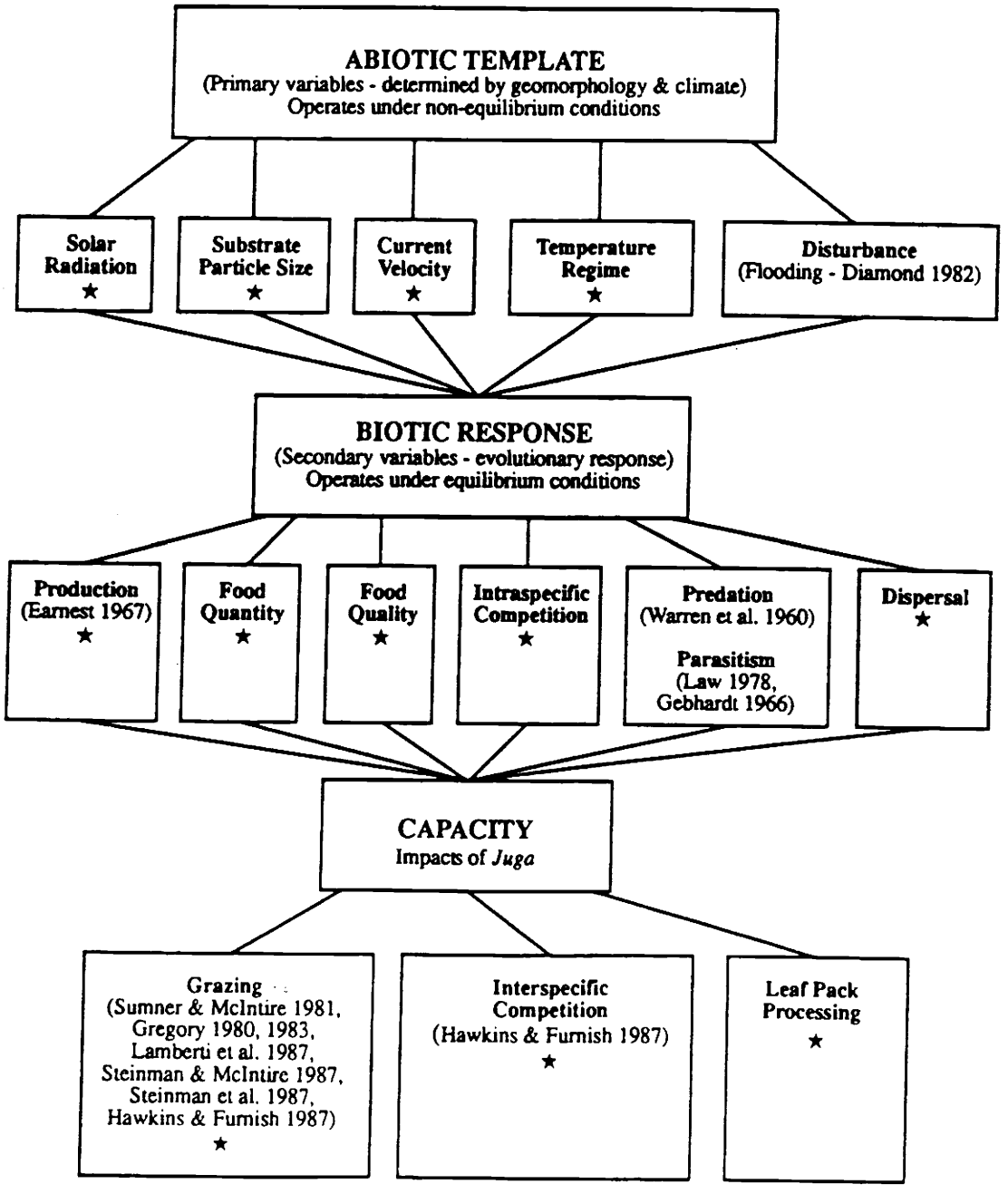


Figure 5.1.

Temperature: Temperature was the primary variable influencing snail growth. Growth was generally positive during the fall, spring and summer, and negative during the winter months. The threshold temperature for growth appears to be about 4°C, or less than 130 degree days accumulated monthly. Feeding behavior was inhibited by cold temperatures and many individuals lost weight during the winter months.

Behavioral responses such as dispersal and microhabitat preferences were also strongly influenced by temperature. During winter months, little or no dispersal was detected and snail biomass was evenly distributed across different shade levels eventhough food abundance, measured as chlorophyll a, was consistently higher in unshaded treatments (Fig. 2.9). Snail biomass was highest on the 10-cm substrate in both summer and winter (Fig. 2.5), so preference for a coarse substrate appears to occur regardless of temperature.

Microhabitat and Snail Distribution: Shade, substrate particle size and current velocity all influenced snail distribution, but the response was dependent upon season and body size. Large snails (and thus the highest biomass) were most abundant in unshaded patches and on coarse substrates during the summer. During the winter, snails still congregated on cobbles but they exhibited no clear preference for any shade treatment. The greatest biomass was nearly always

concentrated on the coarsest particle sizes available (5-10 cm diameter), regardless of season. Selection of microhabitat was size-specific: small snails occurred in finer substrates and in areas of higher shading than did the larger, more mature snails. Accessibility to substrates by *J. silicula* appears to be determined by the size of substrate interstices. Medium to large-sized snails were found primarily on those substrates that were most easily grazed (smooth cobbles) and which had interstitial spaces large enough to accommodate their large body size.

There was a negative relationship between current velocity and snail density. In Oak Creek densities often exceeded 1000 individuals$\cdot m^{-2}$ in slow currents (velocities <30 cm$\cdot sec^{-1}$), they were generally below 100$\cdot m^{-2}$ at current velocities >30 cm$\cdot sec^{-1}$ (Fig. 2.12). Hawkins and Furnish (1987) reported a strong negative correlation between gradient of a stream reach, and both snail density and biomass. These data also indicate that snails avoid fast current velocities, since gradient and current velocity are positively correlated. No relationship between current velocity and snail body size (i.e. shell length) was found.

Growth and Dispersal: Growth and dispersal of snails were dependent upon seasonal variation in temperature, population density, and food quality and quantity. The quantity of food available was in turn determined by

grazing intensity which was a function of snail density. These findings confirm results from laboratory experiments by Gregory (1980), who observed a highly significant relationship between snail growth and standing crop of periphyton. Growth, production and dispersal were all low in the winter. During summer, when temperature was above 5°C and chlorophyll a concentration was greatest, high growth rates and dispersal were observed for most months. Annual growth was significantly higher across all size classes under conditions of reduced snail density. These data demonstrate that growth of *J. silicula* is dependent upon both temperature and food availability.

Laboratory growth rates were positive on a variety of foods confirming *J. silicula's* status as a generalist in its feeding behavior (Hawkins et al. 1983). However, growth was significantly higher on periphyton compared to carrion, wood and alder leaves, suggesting that snail production will be highest in streams where periphyton, mainly composed of diatoms, is plentiful. Although Hawkins and Furnish (1987) reported higher densities of *J. silicula* in stream reaches with an open canopy compared to those that were closed, the differences were not statistically distinguishable. They also reported finding no significant relationship between canopy cover and snail biomass, perhaps because canopy cover was defined on too coarse a scale.

Leaf Processing: The importance of *J. silicula* as a

shredder in streams (Anderson et al. 1978) was confirmed in the study of the snail's impact on rate of weight loss of leaf packs. Processing took almost twice as long when snail density was reduced. Total macroinvertebrate biomass per leaf pack was significantly reduced by snails for the first 70 days of the field experiment. It appears that snails were able to exert this effect by rapid colonization of the unconditioned leaf packs and their high ingestion rates. Feeding by snails increased the rate of leaf processing, and as a result decreased the availability of 1) food for other shredders and 2) habitat for other functional groups.

Although the conversion of leaf litter from CPOM to FPOM was not measured at Oak Creek, it is instructive to compare the Oak Creek study to a similar one that was conducted in a small woodland stream in Tennessee, where the pleurocerid snail, *Elimia* (formerly *Goniobasis*) *clavaeformis* often comprised 50% of the invertebrate biomass. Mulholland et al. (1985) stocked four artificial channels with different densities of *E. clavaeformis* to examine its impact on leaf-litter weight loss and nutrient spiralling. Feeding activity by *Elimia* accelerated loss of CPOM almost three-fold (from 292 to 793 $mg \cdot m^{-2} \cdot d^{-1}$) and the rate at which FPOM accumulated in the stream more than five-fold (from 49 to 279 $mg \cdot m^{-2} \cdot d^{-1}$). However, spiralling length was increased because *Elimia* reduced bacterial populations through its feeding activity and

thereby reduced the mineralization of detritus and whole-stream utilization of phosphorous. Although different measurements were made in the study at Oak Creek, it appears that generalities about *Elimia*'s impact on leaf pack weight loss also apply to *Juga*.

Integration: Several environmental variables must be taken into consideration simultaneously in order to predict the distribution of *J. silicula*, as well as its competitive impact (Table 5.1). The underlying assumption is that the influence of snails will be greatest in microhabitats where their biomass is greatest (i.e. numerous young snails have less impact than a few large adults because they consume less and cause less disturbance as they graze).

Physical factors that influence snail distribution, in order of importance are: temperature, current velocity, substrate particle size and light. Snail abundance in Oak Creek was often greater than $1000 \cdot m^{-2}$ when current velocities were $<30 cm \cdot sec^{-1}$, compared to densities of <100 when current velocities were >30 $cm \cdot sec^{-1}$ (Fig. 2.12). Where the constraint of current velocity is removed, large snails will concentrate their activities in preferred microhabitats characterized by coarse substrates and open canopy. The threshold value for substrate particle size is somewhere in the range from 5 to 10 cm diameter, because snail biomass on cobble (10 cm) was twice that for

Table 5.1. Physical factors affecting the distribution of *Juga silicula* and predicting the impact of grazing by the snail and the intensity of competition between snails and macroinvertebrates based on variation in those physical factors. (Competition is considered to be asymmetrical in the sense that there was no evidence to indicate that snails were impacted by competition with other macroinvertebrates.) See text for explanation.

SEASON/ TEMPERATURE		CURRENT VELOCITY		SUBSTRATE SIZE		CANOPY COVER		BIOMASS OF *Juga*	GRAZING EFFECTS	INTENSITY OF COMPETITION
SUM	WIN	HI ($cm \cdot sec^{-1}$)	LO	COARSE (cm)	FINE	OPEN (%)	CLOSED			
		>30	<30	>5	<5	>75	<75			
+			+	+		+		HIGHEST	HIGHEST	HIGHEST
+			+	+			+	MED	MED	MED
+			+		+	+		MED	MED	MED
+			+		+		+	MED	LOW	LOW
+		+		+		+		LOW	LOW	LOW
+		+		+			+	LOW	LOW	LOW
+		+			+	+		NO HABITAT*		---
+		+			+		+	NO HABITAT*		---
	+		+	+		+		HIGH	LOW	MED
	+		+	+			+	MED	LOW	MED
	+		+		+	+		LOW	LOW	LOW
	+		+		+		+	LOW	LOW	LOW
	+	+		+		+		LOW	LOW	LOW
	+	+		+			+	LOW	LOW	LOW
	+	+			+	+		NO HABITAT*		---
	+	+			+		+	NO HABITAT*		---

* Fine substrates do not co-occur with high current velocity.

any smaller substrate during the winter, and 3 to 5x higher in summer (Fig. 2.5). Canopy cover is also important, but is ranked third because its impact on snail biomass appears to be less than for the other two. This leads to the prediction that snail biomass will be high, and grazing impacts and competitive effects will be high under this combination of conditions when snails are active (i.e. during the summer). During winter months, when snails are inactive, biomass remains high, but grazing and competitive effects will be low.

According to this scheme, taxa that exhibit the greatest degree of overlap in habitat preference with snails will have the greatest response to removal of snails. Hawkins and Furnish (1987) illustrated this relationship by plotting overlap in substrate use between *C. silicula* and the 16 most common taxa (93% of total number) against percent difference in density in the two density treatments (Fig. 5.2). Percent difference in density is defined as (low-high/low) x 100, and expresses the relative effect of snails on specific taxa. If the taxon had a very high abundance in the channel from which snails had been removed compared to its abundance in the channel with snails, the percent difference was high (range from 50 to 150). If snails made no difference, or if the density of a specific taxon was enhanced by their presence, percent difference ranged from 0 to -50. Generally the ratio is greater than zero, indicating that the density of

Fig. 5.2. Relationship between percent substrate overlap (ϕ) and relative effect of snails on densities of 16 invertebrate taxa (r_s=0.64, P<0.02) collected from the artificial channels at Oak Creek, Benton County, Oregon in August of 1983. Percent differences were calculated as ((low-high)/low) x 100. Negative values indicate that densities were highest in the high-density channel. The line was fitted by regression. Solid points are relatively sedentary taxa; open circles are relatively mobile taxa. More sedentary taxa are above the regression line than below and vice versa for mobile taxa (Fisher's exact test, P=0.02). Numbers indicate rank of relative abundance, most=1 and least=16. From Hawkins and Furnish (1987).

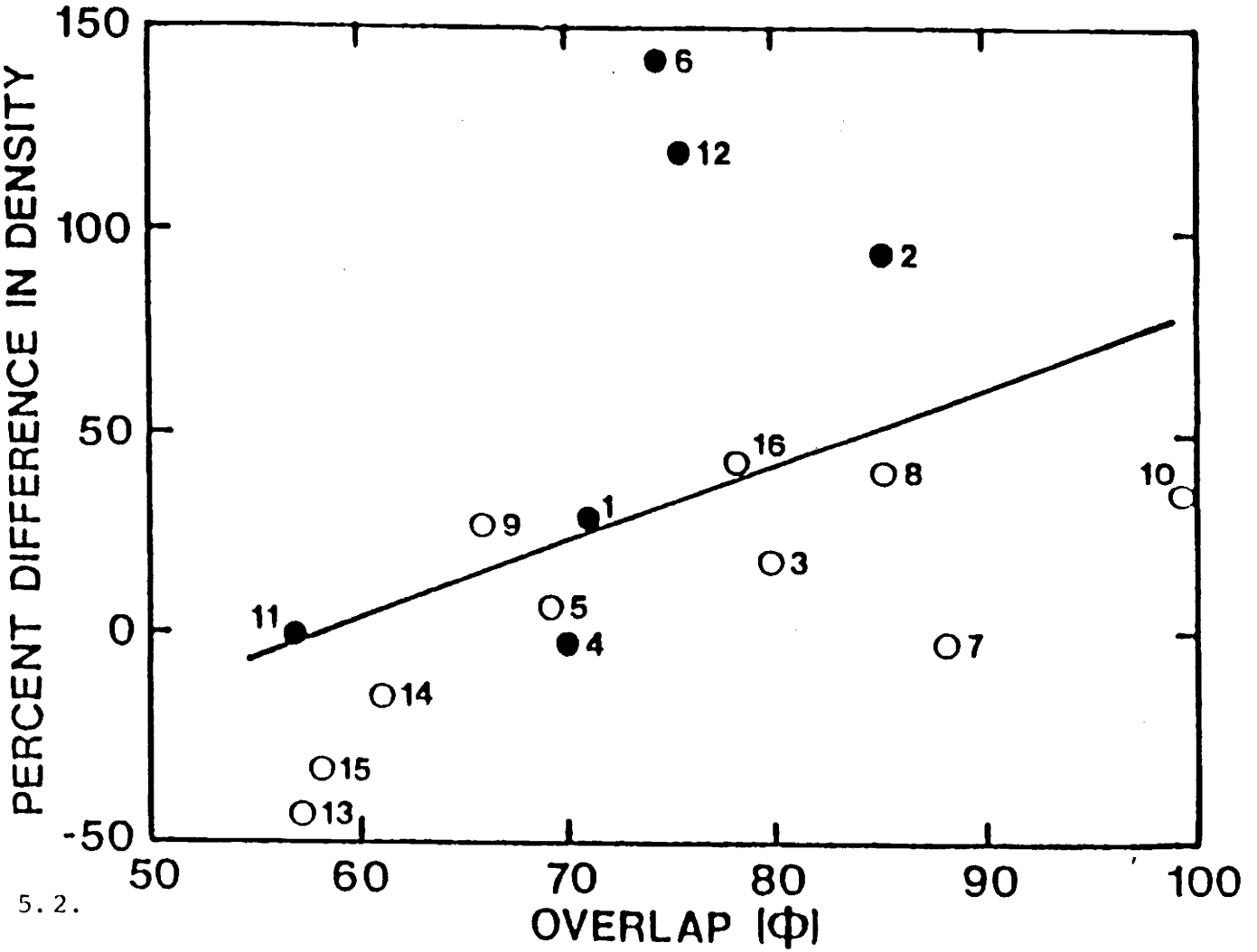

150
100
50
0
-50
PERCENT DIFFERENCE IN DENSITY
50
60
70
80
90
100
OVERLAP |Φ|
6
12
2
16
8
10
1
9
3
5
11
4
7
14
15
13

Figure 5.2.

most taxa was greatest in the snail-removal channel. The figure shows that as substrate overlap increases, so does the ratio (i.e. snails exert an influence commensurate with overlap in substrate resource use). The figure also shows that sedentary taxa are more affected than are mobile taxa. Taxa that responded by moving to a shade treatment favored by *J. silicula* when the snail was removed were *Micropsectra*, *Parametriocnemus*, *Macropelopia*, *Heleniella* (all are chironomid midges, the first of which is sedentary), and Oligochaeta (Hawkins and Furnish 1987, Fig. 4). Further evidence for a shade-specific response to competition was presented in Fig. 2.12. Taxa that apparently shifted their distributions to heavy shade in response to a high density of snails in unshaded patches were the chironomid midges *Micropsectra* and *Stempellinella*, the mayflies *Paraleptophlebia* and *Cinygmula*, and the stonefly *Zapada*. This shade-specific response was observed in the summer, but not in the winter when *J. silicula* was inactive. The response of these taxa was probably due to a combination of exploitative and interference competition. Exploitative competition operates when snails depress food abundance which results in the emigration of other invertebrates. Interference competition operates when grazing activities by snails disturbs and displaces other invertebrates.

The information on natural history and habitat requirements of *J. silicula* make it possible to derive some

generalities to account for the snail's success, (defined as a high relative abundance and biomass) in many lowland stream communities west of the Cascade Mountains, and to speculate on the factors that determine its geographic distribution. Foremost among the reasons for its abundance in many stream communities is its omnivorous food habits. The snail can successfully grow and persist in many habitats where the availability of different foods fluctuates seasonally and/or yearly. Snails are also long-lived with a life span of about 7 years. The slow rate of turnover, relative to many uni- or multi-voltine species, allows a great amount of community biomass to become concentrated in snail tissue. Mortality from predation appears to decrease with size and age, so that the size structure of the population remains relatively stable through time. Snails can survive through the winter because of the phenomenon of degrowth (Russel-Hunter et al. 1984). If snails obtain enough food to accumulate sufficient tissue when conditions are favorable, they can withstand cold periods by using tissue reserves.

A final reason for success is the resource partitioning of microhabitats by snails of different sizes or ages. Females selectively oviposit in shaded areas that are otherwise avoided by adults. Young snails gradually move to unshaded areas, but they still avoid co-occurrence with adults by occupying finer substrates, and perhaps faster current velocities.

The present-day geographic distribution of *J. silicula* has been determined by past geologic events (see Chapter I) and changes in prevailing climate. Since the end of the Cretaceous, approximately 65 mybp, when pleurocerids began to invade freshwater and disperse from the mid-continental seaway to the east and west, there have been major tectonic events and climatic changes that have influenced the family's distribution. In the west, the Pacific coastline gradually moved westward from the Jurassic Period (approximately 150-180 mybp) to the Oligocene Epoch (35 mybp, Alt and Hyndman 1978). Its original position ran from southwestern Oregon in the region of the Klamath Mountains towards the Blue and Wallowa Mountains in the northeast. The earliest record of *Juga silicula* is in northern Idaho from the Miocene Epoch (Taylor 1985b). Fossils indicate that the climate was more humid than at present and the area supported a diverse mesophytic forest similar to the present day forests of the southern Appalachian Mountains (Smiley 1985). Tectonic changes have caused a gradual drying and cooling in what is now eastern Oregon as the maritime influence shifted to the west. Pleurocerids apparently migrated westward to the Klamath Lakes region and the Sacramento drainage via a connection between the Snake and Pit Rivers that is believed to have existed until the Pliocene (13 mybp, Taylor 1985b) and by as yet undeciphered drainages associated with the Columbia, Deschutes and Owyhee Rivers where the subgenus *Calibasis*

occurs today.

I believe that the present day distribution of *J. silicula* is primarily determined by temperature and rainfall. In the north, the growing season for *J. silicula* is too short to allow them to accumulate enough tissue reserves during periods of activity to successfully overwinter. In the south, several factors probably operate to prevent successful establishment of *J. silicula*. Coastal streams of California occur in areas that are too arid to sustain populations (Taylor 1985b).

This study of the natural history of *Juga silicula* has illuminated the means by which physical and seasonal variables influence the growth and distribution of a dominant invertebrate in stream communities of the Pacific Northwest. It has also allowed for the construction of a model that predicts the circumstances under which the impact of the snail will be significant. Patterns of distribution and abundance are clearly affected by the combined influence of the physical and biological environment. It is imperative to understand the contribution of both as stream ecologists attempt to accurately interpret and predict how key factors operate to structure communities. As George Bartholomew (1964) has astutely observed, understanding of principles operating to affect one level of a structural hierarchy, such as a population, are best achieved by elucidation of factors at lower levels (i.e. the physiology or behavior of

individuals) and their significance is manifest at higher levels (the community). According to the conceptual framework presented in Fig. 5.1, the physical environment represents the lowest level of the hierarchy, and an understanding of its effect on the organism may, in turn, be used to explain the variable influence that the snail exerts on community structure and processes.

LITERATURE CITED

Adams, C.C. 1915. The variations and ecological distribution of the snails of the genus *Io*. Memoirs of the National Academy of Science 12(2), 2nd memoir, 92 pp.

Adams, J., J. Gee, P. Greenwood, S. McKelvey and R. Perry. 1987. Factors affecting the microdistribution of *Gammarus pulex* (Amphipoda): an experimental study. Freshwater Biology 17:307-316.

Aldridge, D.W. 1982. Reproductive tactics in relation to life-cycle bioenergetics in three natural populations of the freshwater snail, *Leptoxis carinata*. Ecology 63:196-208.

Alt, D.D. and D.W. Hynman. 1981. Roadside Geology of Oregon. 2nd edition. Montana Press Publishing, Missoula, Montana. 272 pp.

Anderson, N.H. 1976. The distribution and biology of the Oregon Trichoptera. Agricultural Experiment Station Technical Bulletin No. 134. 152 pp.

Anderson, N.H. and E.J. Grafius. 1975. Utilization and processing of allochthonous material by stream Trichoptera. Verhandlungen Internationale Vereinigung für Theoretische und Angewandte Limnologie 19:3022-3028.

Anderson, N.H., J.R. Sedell, L.M. Roberts and F.J. Triska. 1978. The role of macroinvertebrates in processing wood debris in coniferous forest streams. American Midland Naturalist 100:64-82.

Anderson, N.H. and J.R. Sedell. 1979. Detritus processing by macroinvertebrates in stream ecosystems. Annual Review of Entomology 24:351-377.

Baily, J.L.,Jr., R. Pearl and C.P. Winsor. 1933. Variation in *Goniobasis virginica* and *Anculosa carinata* under natural conditions. III. Correlations, shape of shells, and conclusions. Biologia generalis 9(2):48-69.

Baldwin, N.L., R.E. Millemann and S.E. Knapp. 1967. "Salmon poisoning" disease. III. Effect of experimental *Nanophyetus salmincola* infection on the fish host. Journal of Parasitology 53:556-564.

Bärlocher, F. 1980. Leaf eating invertebrates as competitors of aquatic hyphomycetes. Oecologia 47:303-306.

Barnes, J.R., J.V. McArthur and C.E. Cushing. 1986. Effect of excluding shredders on leaf litter Effect decomposition in two streams. Great Basin Naturalist 46:204-207.

Bartholomew, G. A. 1964. The roles of physiology and behavior in the maintenance of homeostasis in the desert environment, pp. 7-29. *In*: Homeostasis and Feedback Mechanisms. (Symposia of the Society for Experimental Biology 18.) Academic Press, Inc., New York. 460 pp.

Bayne, C.J. and E.S. Loker. 1987. Survival within the snail host, pp. 321-346. *In*: D. Rollinson and A. Simpson, (eds). Biology of Schistosomes: From Genes to Latrines. Academic Press, London. 472 pp.

Benfield, E.F. and J.R. Webster. 1985. Shredder abundance and leaf breakdown in an Appalachian Mountain stream. Freshwater Biology 15:113-120.

Behmer, D.J. and C.P. Hawkins. 1986. Effects of overhead canopy on macroinvertebrate production in a Utah stream. Freshwater Biology 16:287-300.

Benke, A.C. 1984. Secondary production of aquatic insects,pp. 289-322. *In*: Resh, V.H. and D.M. Rosenberg, (eds). The Ecology of Aquatic Insects. Praeger Publishers, New York, N.Y. 625 pp.

Bournaud, M. 1963. Le courant, facteur écologique et éthologique de la vie aquatique. Hydrobiologia 21:125-165.

Bovbjerg, R.V. 1965. Feeding and dispersal in the snail *Stagnicola reflexa* (Basommatophora:Lymnaeidae). Malacologia 2:199-207.

Brocksen, R.W., G.E. Davis and C.E. Warren. 1968. Competition, food consumption and production of sculpins and trout in laboratory stream communities. Journal of Wildlife Management 32:51-75.

Burch, J.B. 1982. Freshwater snails (Mollusca: Gastropoda) of North America. U.S. Environmental Protection Agency Publication EPA-600/3-82-026. 294 pp.

Calow, P. 1974. Some observations on locomotory strategies and their metabolic effects in two species of freshwater gastropods, *Ancylus fluviatilis* Mull. and *Planorbis contortus* Linn. Oecologia 16:149-161.

Ching, H. 1957. The morphology of *Oxytrema silicula* (Gould). M.S. Thesis, Oregon State University. 60 pp.

Clarke, A.H. 1981. The Freshwater Molluscs of Canada. National Museum of Natural Sciences, National Museums of Canada, Ottawa, Canada. 446 pp.

Crutchfield, P.J. 1966. Positive rheotaxis in *Goniobasis proxima*. Nautilus 79:80-85.

Cuker, B.E. 1983. Competition and coexistence among the grazing snail *Lymnaea*, Chironomidae, and microcrustacea in an alpine epilithic lacustrine community. Ecology 64:10-15.

Culp, J. M., S.J. Walde and R.W. Davies. 1983. Relative importance of substrate particle size and detritus to stream benthic macroinvertebrate microdistribution. Canadian Journal of Fisheries and Aquatic Sciences 40:1568-1574.

Cummins, K.W., R.C. Petersen, F.O. Howard, J.C. Wuycheck and V.I. Holt. 1973. The utilization of leaf litter by stream detritivores. Ecology 54:336-345.

Cummins, K.W., G.L. Spengler, G.M. Ward, R.M. Speaker, R.W. Ovink, D.C. Mahan and R.L. Mattingly. 1980. Processing of confined and naturally entrained leaf litter in a woodland stream ecosystem. Limnology and Oceanography 25:952-957.

Dazo, B.C. 1965. The morphology and natural history of *Pleurocera acuta* and *Goniobasis livescens* (Gastropoda: Ceritheacea:Pleuroceridae). Malacologia 3:1-80.

Diamond, J. 1977. The population dynamics and reproductive strategy of the stream snail, *Oxytrema silicula* (Gould) in relation to stream order. M.S. Thesis, Oregon State University. 77 pp.

Diamond, J. 1982. Stream geomorphology and benthic habitat predictability as determinants of the population dynamics and life history of the snail *Juga plicifera*. Journal of Freshwater Ecology 1:577-588.

Douglas, B. 1958. The ecology of the attached diatoms and other algae in a small stony stream. Journal of Ecology 46:295-322.

Downing, J.A. 1984. Assessment of secondary production: the first step, pp. 1-18. *In*: J.A. Downing and F.H. Rigler, (eds). A Manual on Methods for the Assessment of Secondary Productivity in Freshwaters. 2nd edition. IBP Handbook No. 17. Blackwell Scientific Publications, Inc., Oxford. 501 pp.

Downing, J.A. and F.H. Rigler. 1984. The calculation of secondary production, pp 161-227. *In*: J.A. Downing and F.H. Rigler, (eds). A Manual on Methods for the Assessment of Secondary Productivity in Freshwaters. 2nd edition. IBP Handbook No. 17. Blackwell Scientific Publications, Inc., Oxford. 501 pp.

Earnest, R. 1967. Production of the snail *Oxytrema silicula* (Gould) in an experimental stream. M.S., Oregon State University. 51 pp.

Eastburn, R.L., T.R. Fritsche and C.A. Terhune,Jr. 1987. Human intestinal infection with *Nanophyetus salmincola*. American Journal of Tropical Medicine and Hygiene 36:586-591.

Eisenberg, R.M. 1966. The regulation of density in a natural population of the pond snail, *Lymnaea elodes*. Ecology 47:889-906.

Elliott, J.M. 1977. Some Methods for the Statistical Analysis of Samples of Benthic Invertebrates. 2nd edition. Freshwater Biological Association Scientific Publication No. 25. 160 pp.

Elwood, J.W., J.D. Newbold, A.F. Trimble and R.W. Stark. 1981. The limiting role of phosphorus in a woodland stream ecosystem: effects of P enrichment on leaf decomposition and producers. Ecology 62:146-158.

Foin, T.C. 1967. The comparative dynamics of populations of the freshwater operculate snail, *Goniobasis proxima*. Ph.D. Dissertation, University of North Carolina, Chapel Hill, North Carolina.

Gebhardt, G.A. 1966. Studies on the molluscan and fish hosts of the "salmon poisoning" fluke, *Nanophyetus salmincola* (Chapin). M.S. Thesis, Oregon State University. 151 pp.

Gee, J.H.R. 1982. Resource utilization by *Gammarus pulex* (Amphipoda) in a Cotswold stream: a micro-distribution study. Journal of Animal Ecology 51:817-832.

Golladay, S.W., J.R. Webster and E.F. Benfield. 1983. Factors affecting food utilization by a leaf shredding aquatic insect: leaf species and conditioning time. Holarctic Ecology 6:157-162.

Goodrich, C. 1942a. The Pleuroceridae of the Atlantic Coastal Plain. Occasional Papers of the Museum of Zoology, University of Michigan 456:1-6.

Goodrich, C. 1942b. The Pleuroceridae of the Pacific Coastal drainage, including the western interior basin. Occasional Papers of the Museum of Zoology, University of Michigan 469:1-4.

Goodrich, C. 1944. Pleuroceridae of the Great Basin. Occasional Papers of the Museum of Zoology, University of Michigan 485:1-11.

Gore, J.A. 1983. Considerations of size related flow preferences among macroinvertebrates used in instream flow studies, pp 389-397. *In*: Developments in Ecology and Environmental Quality, Volume II, Balaban International Publications, Jerusalem.

Gould, A.A. 1847. Descriptions of *Melania*, from the collection of the Exploring Expedition. Proceedings of the Boston Society of Natural History 2:222-225.

Gregory, S.V. 1980. Effects of light, nutrients and grazing on periphyton communities in streams. Ph.D. Dissertation, Oregon State University. 151 pp.

Gregory, S.V. 1983. Plant-herbivore interactions in stream ecosystems, pp 157-189. *In*: J.R. Barnes and G.W. Minshall, (eds). Stream Ecology: Applications and testing of General Ecological Theory. Plenum Press, New York, N.Y. 399 pp.

Hanson, B. J., K.W. Cummins, A.S. Cargill II and R.W. Lowry. 1983. Dietary effects on the lipid and fatty acid composition of *Clistoronia magnifica* (Trichoptera: Limnephilidae). Freshwater Invertebrate Biology 2:2-15.

Harman, W.N. 1972. Benthic substrates: Their effect on freshwater Mollusca. Ecology 53:271-277.

Hart, D.D. 1981. Foraging and resource patchiness: field experiments with a grazing stream insect. Oikos 37:46-52.

Hart, D.D. 1984. The importance of competitive interactions within stream populations and communities, pp. 99-136. *In*: J.R. Barnes and G.W. Minshall, (eds). Stream Ecology: Applications and Testing of General Ecological Theory. Plenum Press, New York, N.Y. 399 pp.

Hart, S.D.and R.P. Howmiller. 1975. Studies on the decomposition of allochthonous detritus in two southern California streams. Verhandlungen Internationale Vereinigung für Theoretische und Angewandte Limnologie 19:1665-1674.

Hawkins, C.P., M.L. Murphy, N.H. Anderson and M.A. . Wilzbach. 1983. Density of fish and salamanders in relation to riparian canopy and physical habitat in streams of the northwestern United States. Canadian Journal of Fisheries and Aquatic Sciences 40:1173-1185.

Hawkins, C.P. and J.K. Furnish. 1987. Are snails important competitors in stream ecosystems? Oikos 49:209-220.

Hemphill, N. and S.D. Cooper. 1983. The effect of physical disturbance on the relative abundance of two filter feeding insects in a small stream. Oecologia (Berlin) 58:378-382.

Henderson, J. 1929. Non-marine Mollusca of Oregon and Washington. University of Colorado Studies 17(2):47-190.

Henderson, J. 1935. West American species of *Goniobasis*, with descriptions of new forms. Nautilus 48:94-99.

Hill, W.R. and A.W. Knight. 1987. Experimental analysis of the grazing interaction between a mayfly and stream algae. Ecology 68:1955-1965.

Hocutt, C.H. and E.O. Wiley. 1986. The Zoogeography of North American Freshwater Fishes. John Wiley & Sons, New York. 866 pp.

Houp, K.H. 1970. Population dynamics of *Pleurocera acuta* in a central Kentucky limestone stream. American Midland Naturalist 83:81-88.

Hubbard, E.F., F.A. Kilpatrick, L.A. Martens and J.F. Wilson, Jr. 1982. Measurement of time of travel and dispersion in streams by dye-tracing, pp. 259-270. *In*: Techniques of Water Resources Investigations of the U.S. Geological Survey. Chapter A9, Book 3.

Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54:187-211.

Hynes, H.B.N. 1970. The Ecology of Running Waters. University Press, Toronto. 555 pp.

Illies, J. 1975. A new attempt to measure production in running waters. Schlitz studies on productivity, No. 12. Verhandlungen Internationale Vereinigung für Theoretische und Angewandte Limnologie 19:1705-1711.

Iversen, T.M. 1974. Ingestion and growth in *Sericostoma personatum* in relation to the nitrogen content of

ingested leaves. Oikos 25:278-282.

Kauffman, K.W. 1981. Fitting and using growth curves. Oecologia 49:293-299.

Kaushik, N.K. and H.B.N. Hynes. 1971. The fate of the dead leaves that fall into streams. Archives für Hydrobiologie 68:465-515.

Krueger, C.C. and T.F. Waters. 1983. Annual production of macroinvertebrates in three streams of different water quality. Ecology 64:840-850.

Krieger, K.A. and W.D. Burbanck. 1976. Distribution and dispersal mechanisms of *Oxytrema (=Goniobasis) suturalis* Haldeman (Gastropoda:Pleuroceridae) in the Yellow River, Georgia, U.S.A. American Midland Naturalist 95:49-63.

Lamberti, G.A. and V.H. Resh. 1983. Stream periphyton and insect herbivores: an experimental study of grazing by a caddisfly population. Ecology 64:1124-1135.

Lamberti, G.A. and J.W. Moore. 1984. Aquatic insects as primary consumers, pp. 164-195. *In*: V.H. Resh and D.M. Rosenberg, (eds). The Ecology of Aquatic Insects, Praeger Publishers, New York, N.Y. 625 pp.

Lamberti, G.A., L.R. Ashkenas, S.V. Gregory and A.D. Steinman. 1987. Effects of three herbivores on periphyton communities in laboratory streams. Journal of the North American Benthological Society 6:92-104.

Laville, H. 1971. Recherches sur les Chironomides (Diptera) lacustres du massif de Neouvieille (Haute-Pyrenees). Premiere partie: Systematique, Ecologie, Phenologie. Annales de Limnologie 7:173-332.

Law, D.T. 1976. Studies on some digenetic trematodes from Ritner Creek, Polk County, Oregon. Dissertation, Oregon State University. 210 pp.

Leopold, L., M.G. Wolman and J.P. Miller. 1964. Fluvial Processes in Geomorphology. W.H. Freeman, San Francisco California, U.S.A. 522 pp.

Lorenzen, C.J. 1967. Determination of chlorophyll and pheopigments:spectrophotometric equations. Limnology and Oceanography 12:343-346.

Mackay, R.J. and J. Kalff. 1973. Ecology of two related species of caddisfly larvae in the organic substrates of a woodland stream. Ecology 54:499-511.

Mancini, E.R. 1978. The biology of *Goniobasis semicarinata* (Say) (Gastropoda:Pleuroceridae) in the Mosquito Creek drainage system, southern Indiana. Dissertation. University of Louisville, Louisville, Kentucky. 93 pp.

Marker, A.F.H. and S. Jinks. 1982. The spectrophotometric analysis of chlorophyll a and phaeopigments in acetone ethanol and methanol. Archives für Hydrobiologie, Beihefte 16:3-17.

McAuliffe, J.R. 1984. Competition for space, disturbance and the structure of a benthic stream community. Ecology 65:894-908.

McMahon, R.F., R.D. Hunter and W.D. Russell-Hunter. 1974. Variation in aufwuchs at six freshwater habitats in terms of carbon biomass and carbon:nitrogen ratio. Hydrobiologia 45:391-404.

Merritt, R.W. and K.W. Cummins. 1984. An Introduction to the Aquatic Insects of North America. 2nd edition. Kendall/Hunt Publishing Company, Dubuque, Iowa. 722 pp.

Minckley, W.L., D.A. Hendrickson and C.E. Bond. 1986. Geography of western North American freshwater fishes: Description and relationships to intracontinental tectonism, pp. 519-613. *In*: C.H. Hocutt and E.O. Wiley, (eds). The Zoogeography of North American Freshwater Fishes. John Wiley and Sons, New York. 866 pp.

Minshall, G.W. 1967. Role of allochthonous detritus in the trophic structure of a woodland springbrook community. Ecology 48:139-149.

Minshall. G.W. 1984. Aquatic insect-substratum relationships, pp. 358-400. *In*: V.H. Resh and D.M. Rosenberg, (eds). The Ecology of Aquatic Insects, Praeger Publishers, New York, N.Y. 625 pp.

Minshall, G.W. and R. C. Petersen, Jr. 1985. Towards a theory of macroinvertebrate community structure in stream ecosystems. Archives für Hydrobiologie 104:49-76.

Mulholland, P.J., J.W. Elwood, J.D. Newbold and L.A. Ferren. 1985. Effect of a leaf-shredding invertebrate on organic matter dynamics and phosphorus spiralling in heterotrophic laboratory streams. Oecologia 66:199-206.

Neves, R.J. 1979. Secondary production of epilithic fauna in a woodland stream. American Midland Naturalist 102:209-224.

Otto, C. 1974. Growth and energetics in a larval population of *Potamophylax cingulatus* (Steph.) in a south Swedish stream. Journal of Animal Ecology 43:339-361.

Paine, R.T. 1966. Food web complexity and species diversity. American Naturalist 100:65-75.

Paine, R.T. 1980. Food webs: linkages, interaction strength and community infrastructure. Journal of Animal Ecology 49:667-685.

Patrick, R. 1970. Benthic stream communities. American Scientist 58:546-549.

Patrick, R. 1975. Structure of stream communities, pp. 445-459. *In*: M.L. Cody and J.M. Diamond, (eds). Ecology and Evolution of Communities. Belknap Press, Harvard University, Cambridge, Mass. 545 pp.

Petersen, R.C.,Jr. and K.W. Cummins. 1974. Leaf processing in a woodland stream. Freshwater Biology 4:343-368.

Pollard, R.A. 1955. Measuring seepage through salmon spawning gravel. Canadian Journal of Fisheries and Aquatic Sciences 12:706-741.

Power, M.E., R.J. Stout, C.E. Cushing, P.P. Harper, F.R. Hauer, W.J. Matthews, P.B. Moyle, B. Statzner and I.R. Wais De Badgen. 1988. Biotic and abiotic controls in river and stream communities. Journal of the North American Benthological Society 7:456-479.

Pringle, C.M. 1982. Factors affecting the microdistribution of different sizes of the amphipod *Gammarus pulex*. Oikos 38:369-373.

Pringle, C.M., R.J. Naiman, G. Bretschko, J.R. Karr, M.W. Oswood, J.R. Webster, R.L. Welcomme and M.J. Winterbourn. 1988. Patch dynamics in lotic ecosystems: the stream as a mosaic. Journal of the North American Benthological Society 7:503-524.

Reice, S.R. 1974. Environmental patchiness and the breakdown of leaf litter in a woodland stream. Ecology 55:1271-1282.

Resh, V.H., A.V. Brown, A.P. Covich, M.E. Gurtz, H.W. Li, G.W. Minshall, S.R. Reice, A.L. Sheldon, J.B. Wallace and R. Wissmar. 1988. The role of disturbance in stream ecology. Journal of the North American Benthological Society 7:433-455.

Richardson, T.D., J. F. Scheiring and K.M. Brown. 1988. Secondary production of two lotic snails (Pleuroceridae: *Elimia*). Journal of the North American Benthological Society 7:234-245.

Rigler, F.H. and J.A. Downing. 1984. The calculation of secondary productivity, pp 19-58. *In*: J.A. Downing and F.H. Rigler, (eds). A Manual on Methods for the Assessment of Secondary Productivity in Freshwaters. 2nd edition. IBP Handbook No. 17. Blackwell Scientific Publications, Inc., Oxford.

Ross, M.J. and G.R. Ultsch. 1980. Temperature and substrate influences on habitat selection in two pleurocerid snails (*Goniobasis*). American Midland Naturalist 103:209-217.

Russell-Hunter, W.D. and D.E. Buckley. 1983. Actuarial bioenergetics of nonmarine molluscan productivity, pp. 464-503. *In*: W.D. Russell-Hunter (ed). The Mollusca, Vol. 6 Ecology. Academic Press, Inc. 695 pp.

Sedell, J.R.. F.J. Triska and N.S. Triska. 1975. The processing of conifer and hardwood leaves in two coniferous forest streams. I. Weight loss and associated invertebrates. Verhandlungen Internationale Vereinigung für Theoretische und Angewandte Limnologie 19:1617-1627.

Sheldon, A.L. 1977. Colonization curves: application to stream insects on semi-natural substrates. Oikos 28:256-261.

Short, R.A. and J.V. Ward. 1980. Leaf litter processing in a regulated Rocky Mountain stream. Canadian Journal of Fisheries and Aquatic Sciences 37:123-127.

Siegfried, C.A. and A.W. Knight. 1977. The effects of washout in a Sierra foothill stream. American Midland Naturalist 98:200-207.

Smiley, C.J. (ed.). Late Cenozoic History of the Pacific Northwest. American Association for the Advancement of Science Symposium. 417 pp.

Snedecor. G.W. and W.G. Cochran. 1982. Statistical Methods. Seventh edition. Iowa State University Press, Ames, Ia. 507 pp.

Sokal, R.R. and F.J. Rohlf. 1981. Biometry. 2nd edition. Freeman, San Francisco, Cal.

Speir, J.A. 1975. The ecology and production dynamics of four black fly species (Diptera:Simuliidae) in western Oregon streams. Dissertation, Oregon State University,

297 pp.

Statzner, B. and B. Higler. 1986. Stream hydraulics as a major determinant of benthic invertebrate zonation patterns. Freshwater Biology 16:127-139.

Statzner, B., J.A. Gore and V.H. Resh. 1988. Hydraulic stream ecology: observed patterns and potential applications. Journal of the North American Benthological Society 7:307-360.

Steinman, A.D. and C.D. McIntire. 1987. Effects of irradiance on the community structure and biomass of algal assemblages in laboratory streams. Canadian Journal of Fisheries and Aquatic Sciences 44:1640-1648.

Steinman, A.D., C.D. McIntire, S.V. Gregory, G.A. Lamberti and L.R. Ashkenas. 1987. Effects of herbivore type and density on taxonomic structure and physiognamy of algal assemblages in laboratory streams. Journal of the North American Benthological Society 6:175-188.

Stout, R.J. and W.H. Taft. 1985. Growth patterns of a chironomid shredder on fresh and senescent Tag Alder leaves in two Michigan streams. Journal of Freshwater Ecology 3:147-153.

Streit, B. 1981. Food searching and exploitation by a primary consumer (*Ancylus fluviatilus*) in a stochastic environment: nonrandom movement patterns. Revue suisse Zool. 88:887-895.

Sumner, W.T. and C.D. McIntire. 1982. Grazer-periphyton interactions in laboratory streams. Archives für Hydrobiologie 93:135-157.

Taylor, D.W. 1966. Summary of North American Blancan nonmarine mollusks. Malacologia 4:1-172.

Taylor, D.W. 1981. Freshwater mollusks of California: A distributional checklist. California Fish and Game 67:140-163.

Taylor, D.W. 1985a. Miocene freshwater mollusks from the Clarkia fossil site, Idaho, pp. 73-74. *In*: C.J. Smiley (ed.). Late Cenozoic History of the Pacific Northwest. American Association for the Advancement of Science Symposium. 417 pp.

Taylor, D.W. 1985b. Evolution of freshwater drainages and molluscs in western North America, pp. 265-321. *In*: C.J. Smiley (ed.). Late Cenozoic History of the Pacific Northwest. American Association for the Advancement of Science Symposium. 417 pp.

Taylor, D.W. and G.R. Smith. 1981. Pliocene molluscs and fishes from northeastern California and northwestern Nevada. University of Michigan Museum of Paleontology. Contribution 25:339-413.

Tolkamp, H.H. 1980. Organism-substrate relationships in lowland streams. Agricultural Research Report 907, Agricultural University, Wagenigen, The Netherlands. 211 pp.

Townes, D.R. 1981. Effects of artificial shading on periphyton and invertebrates in a New Zealand stream. New Zealand Journal of Marine and Freshwater Research 15:185-192.

Townsend, C.R. 1989. The patch dynamics concept of stream community ecology. Journal of the North American Benthological Society 8:36-50.

Triska, F.J., J.R. Sedell, B. Buckley. 1975. The processing of conifer and hardwood leaves in two coniferous forest streams. II. Biochemical and nutrient changes. Verhandlungen Internationale Vereinigung für Theoretische und Angewandte Limnologie 19:1628-1639.

Vermeij, G.J. and A.P. Covich. 1978. Coevolution of freshwater gastropods and their predators. American Naturalist 112:833-843.

Wallace, J.B., J.R. Webster and T.F. Cuffney. 1982. Stream detritus dynamics: Regulation by invertebrate consumers. Oecologia 53:197-200.

Warren, C.E. 1971. Biology and Water Pollution Control. W.B. Saunders Co., Philadelphia, Pa. 434 pp.

Warren, C.E., F.J. Burgess, H.K. Phinney, J.D. Lattin and J.H. Wales. 1960. Ecological studies of an experimental stream (Progress Report). Oregon State College Agriculture Experiment Station and Engineering Experiment Station.

Warren, C.E., J.H. Wales, G.E. Davis and P. Doudoroff. 1964. Ecological studies of an experimental stream enriched with sucrose. Journal of Wildlife Management 28:617-660.

Waters, T.F. 1977. Secondary production in inland waters. Advances in Ecological Research 10:91-164.

Webster, J.R. and E.F. Benfield. 1986. Vascular plant breakdown in freshwater ecosystems. Annual Review of Ecology and Systematics. 17:567-594.

White, C.A. 1883. A review of non-marine fossil Mollusca of North America, pp.403-550. *In*: Third Annual Report, Natural History, U.S. Geological Survey, 1881-1882.

Wiley, M.J. and S.L. Kohler. 1981. An assessment of biological interactions in an epilithic stream community using timelapse cinematography. Hydrobiologia 78:183-188.

Wiley, M.J. and S.L. Kohler. 1984. Behavioral adaptations of aquatic insects, pages 101-133. *In*: V.H. Resh and D.M. Rosenberg, (eds). The Ecology of Aquatic Insects. Praeger Publishers, New York, N.Y. 625 pp.

Wright, H.P. 1932. Aquatic Mollusca of the Tippecanoe River system. Part I. Post-glacial migration and present distribution of four species of snails. Ecological Monographs 2:233-259.

APPENDICES

Appendix A. Weight and length conversions used for *Juga silicula*.

Tissue DW (gm) = 0.17004 (Total DW (gm)) - 0.0063

n=117, r^2=0.68

Tissue AFDM (gm) = 0.063061 (Total FW (gm)) + 0.0027,

n=69, r^2=0.84

Total Body AFDM (mg) = 8.13378 (Shell length (cm))$^{3.09654}$

n=30, r^2=0.96

Total FW (mg) = 85.736 (Shell length (cm))$^{2.58015}$,

n=30, r^2=0.93

AFDM tissue (gm) = 0.24038 (Total DW (gm))$^{1.32882}$,
n=13, r^2=0.96

Total AFDM (gm) = -0.018 + 0.28044 (Total DW (gm)),

n=29, r^2=0.96

Total DW (gm) = 0.585595 (Total Wet wt.(gm))$^{1.00796}$,

n=10, r^2=0.99

Total Body AFDM (mg) = -4.09419 + 0.15031 (Total FW (mg)),

n=26, r^2=0.99

AFDM tissue (gm)= 0.909263 (DW tissue (gm)),

n=10, r^2=0.99

Appendix B. COLLECTION LOCALITIES FOR *Juga silicula* (Gould 1847)
Type locality: Nisqually River near Tacoma, Washington

Compiled by J. L. Furnish November 24, 1988
Terry Frest provided records from the Burke Museum, University of Washington, Seattle, Washington, and Timothy Pierce of the Department of Paleontology, University of Michigan, Ann Arbor, Michigan provided additional collection localities..

OREGON

Benton Co.
Marys R. at confluence with Willamette R. (44.55N,123.25W)
Marys R. at Avery Park, Corvallis (45.55N,123.27W)
Marys R. at 53rd St. Bridge, SW of Corvallis (44.50N,123.32W)
Marys River at Bell Fountain Rd. (44.52N,123.33W)
Marys R. at Philomath (44.53N,123.40W)
Marys R. at S. Philomath Rd. (44.52N,123.37W)
Marys R. on Marys River Estate Road (44.55N,123.38W)
Marys R. at Wren on Harris Rd. (T11S,R6W,S28,NW)
Marys R. at Alder (T11S,R7W,S26,SW)
Marys R. at Summit (T11S,R7W, ,NW)
Woods Cr. @ 2 mi. ab. confluence with Marys R.
East Fork of Marys R. (T10S,R7W,S26,NW)
Luckiamute R. at Alexander Rd. (44.41N,123.28W)
Rock Cr. at Hwy. 34 (44.30N,123.27W)
Stilson Cr. Trib. of Rock Cr.
Connection Creek at Rd. 3405 Trib. of Rock Cr.
Connection Creek Headwaters " " " "
1st order Cr. Clear Cut Sale #38 Trib. " "
Tributary A Headwaters " " "
Tributary at end of Rd.#116-3409 " " "
Soap Cr. (44.65N,123.57W)
Berry Creek (44.43N,123.18W)
Tobe Cr. (44.34N,123.57W)
Bob Cr.
Bull Run Cr.
Oak Cr. (44.60N,123.33W)
Oak Cr. East Fork (44.62N,123.32W)
Oak Cr. West Fork (44.63N,123.35W)
S. Fk. Alsea R. 2.8 mi. below Alsea Falls (44.21N,123.32W)

Clackamas Co.
Gribble Cr. (45.25N,122.69W)

Columbia Co.
Merrill Cr. (45.94N,122.85W)

Curry Co.
Blackberry Creek, Trib. of Elk R. (BW)
(42.42N,124.14W)
Douglas Co.
Spencer Cr. (43.78N,123.92W)
Bear Creek. (43.64N,123.34W)
Gassy Cr. (43.42N,123.10W)
Carter Lake, Oregon Dunes Nat'l. Rec. Area
(43.85N,124.15W)
Elk Cr. 3.9 mi. ab. confl. w/ S. Umpqua
(42.91N,122.92W)
S. Umpqua R. at Dumont Cr. (43.03N,122.81W)
S. Umpqua R. @ 4 mi. ab. Tiller (42.97N,122.88W)
Boulder Cr. @ 1 mi. ab. confl. w/S. Umpqua R.
(43.06N,122.77W)
Looking Glass Cr., Winston (43.11N,123.62W)
Tahkenich Lake (43.78N,124.12W)
W.Fk. Smith R., 2.2 mi. ab. confl. w/ Smith R.
(43.83N,123.77W)
Josephine Co.
Fall Cr. nr. confl. w/Ill. R. 10 mi. W. of Selma
(42.30N,123.75W)
Lane Co.
Cook Cr., 1 mi. from confluence w/Blue R.
Fawn Creek (43.92N,122.41W)
Hagen Cr., Trib. of McKenzie
Hammer Cr. (44.21N,123.69W)
Lake Cr., 9.7 mi. ab. confluence w/ Siuslaw R.(GWC)
Long Tom R. at Elmira (Unusual shell-Taylor)
Lookout Cr. at 420 m.
Mack Cr. at 830 m. (44.22N,122.17W)
McKenzie R. at 410 m.
Mill Cr. (43.92N,122.41W)
N. Fk. Quartz Cr. (Riparian Site)
Rainbow Cr. (44.21N,123.69W)
Rock Cr. (44.18N,124.10W)
Spout Cr. (44.05N,123.81W)
Jackson Co.
Rogue R., 1.3 mi. ab. Trail (42.64N,122.77W)
Lincoln Co.
Elkhorn Cr. (44.45N,124.05W)
Flynn Creek 16 km from coast,209 m elevation
(44.53N,123.87W)
Tributary of the Alsea R., near Denzer Bridge
(44.35N,123.82W)
Siletz R. at confluence with Sunshine Cr.
(44.82N,123.77W)
Siletz R. at Sam Cr. Bridge, 4.7 mi. ab. Siletz
(44.67N,123.51W)
Siletz R. at Mack Landing(Gebhardt)
(44.52N,123.57W)
Yaquina R. at Elk City(Gebhardt) (44.62N,123.87W)
Yaquina R. at Eddyville(Diamond) (44.63N,123.78W)

Salmon Cr. @ 3 mi. E of Eddyville on Hyw 20
Drift Cr. in Wilderness area (44.45N,123.92W)
Alsea R. at Tidewater(Gebhardt) (44.40N,123.90W)

Linn Co.
Nr. mouth of Dobbin Cr. Trib. of S. Santiam (44.38N,122.47W)

Marion Co.
S. Fk. of Silver Cr. at Silver Falls St.Pk. (44.88N,122.65W)

Multnomah Co.
Lower Waukeena Cr. at railroad tressel.

Tillamook Co.
Bays Cr. 1.7 mi. ab. confl. w/Nestucca R.

Washington Co.
Gales Cr. 1 mi. N. of Glennwood
McKay Cr. (45.66N,122.98W)

WASHINGTON

Clark Co.
Salmon Cr., 7 mi. N. of Vancouver (45.71N,122.65W)

Cowlitz Co.
Cowlitz R., 8 mi. N. of Castle Rock (J. Hend) (46.60N,123.30W)
Cowlitz R., 8 mi. NW of Kelso (J. Hend) (46.23N,122.90W)

Grays Harbor Co.
A pond on Aberdeen Rd., 5 mi. E. of Elma (J. Hend) (47.50N,123.32W)
Wynrotche R., 1 mi. W. of Montesano (J. Hend) (46.97N,123.63W)
Cloquallum Cr., E. of Elma (J. Hend) (47.30N,123.37W)
Caldwell Cr., Wynoochee Valley(Br.)
Cranberry Creek E. of Ocean City (47.08N,124.12W)
Fairchild Cr., Trib of Humptulips R. (47.20N,123.93W)
Humptulips R. (47.22N,123.92W)
Lunch Cr. (Pierce) (47.47N,124.05W))
Small Spring trib. of Black R. nr. Greys Harbor(Br.)

Jefferson Co.
Quinault R. above Lake Quinault (Pierce) (47.49N,123.80W)

Klickitat Co.
Major Cr. (45.72N,121.33W)

Lewis Co.
Newaukum R., 13 mi. N. of Toledo (J. Hend) (46.60N,122.87W)
Salmon R. 1 mi. S. of Toledo (J. Hend) (46.42N,122.83W)

Mason Co.
Mill Cr. at Shelton (J. Hend) (47.18N,123.10W)
E. Fk. Satsop R., Schafer St. Pk. (47.10N,123.47W)
Skokomish R., 0.5 km. ab. mouth (47.33N,123.13W)
Goldsborough Cr. (Pierce) (47.22N,123.18W)
Kennedy Cr. (Pierce) (47.05N,123.17W)
Rock Cr. (Pierce) (47.17N,123.18W)
Shumacher Cr. (Pierce) (47.32N,122.98W)
Skookum Cr. (Pierce) (47.12N.123.17W)
Perry Cr. (Pierce) (47.05n,123.03w)
Pierce Co.
Murray Cr. at Camp Murray(nr. Tillicum) (J. Hend) (47.10N,122.53W)
Sequalitchew Cr. (Pierce) (47.10N,122.62W)
Skamania Co.
Flume Cr. at Rt. 14(BW) (10 mi east of Stevenson)
Thurston Co.
Black R., Chehalis Indian Res. (46.82N,123.18W)
Rt. 8 Rest Stop, 5 mi. W of Olympia (Pierce) (47.05N,123.02W)
Scatter Cr., nr. Tenino (46.87N,122.87W)
Summit Lake (Pierce) (47.06N,123.13W)

CALIFORNIA

Del Norte Co.
Fern Canyon Cr. (41.38N,124.07W)
Hardscabble Cr. at Hyw. 101 (41.85N,124.02W)
Smith R. at Jed Smith Redwoods. St. Pk. (41.80N,124.08W)
Smith R. at Gasquet (41.85N,123.97W)
Humboldt Co.
Copper Cr. (41.13N,124.80)
Little Lost Man Cr. (41.30N,124.63W)
Harry Weir Creek (41.13N,124.80W)
Lower Trinity R. (Taylor, 1981)
Siskiyou Co.
Klamath R. at Intersection with Interstate 5 and Hwy. 96