

1979

Notes on the comparative ecology of *Cottus bairdi* and *Cottus girardi* in Naked Creek, Virginia

Richard Edmond Matheson
College of William & Mary - Arts & Sciences

Follow this and additional works at: <https://scholarworks.wm.edu/etd>



Part of the [Fresh Water Studies Commons](#)

Recommended Citation

Matheson, Richard Edmond, "Notes on the comparative ecology of *Cottus bairdi* and *Cottus girardi* in Naked Creek, Virginia" (1979). *Dissertations, Theses, and Masters Projects*. Paper 1539625052.
<https://dx.doi.org/doi:10.21220/s2-1pkc-h165>

This Thesis is brought to you for free and open access by the Theses, Dissertations, & Master Projects at W&M ScholarWorks. It has been accepted for inclusion in Dissertations, Theses, and Masters Projects by an authorized administrator of W&M ScholarWorks. For more information, please contact scholarworks@wm.edu.

NOTES ON THE COMPARATIVE ECOLOGY OF COTTUS BAIRDI
" AND COTTUS GIRARDI IN NAKED CREEK, VIRGINIA

A Thesis

Presented to

The Faculty of the Department of Biology
The College of William and Mary in Virginia

In Partial Fulfillment

Of the Requirements for the Degree of
Master of Arts

by

Richard Edmond Matheson, Jr.

1979

APPROVAL SHEET

This thesis is submitted in partial fulfillment of
the requirements for the degree of

Master of Arts

Richard Edmond Matheson, Jr.
Richard Edmond Matheson, Jr.

Approved, August 1979

Garnett R. Brooks, Jr.
Garnett R. Brooks, Jr.

Gregory M. Capelli
Gregory M. Capelli

Mitchell A. Byrd
Mitchell A. Byrd

TABLE OF CONTENTS

	Page
ACKNOWLEDGMENTS.	v
LIST OF TABLES.	vii
LIST OF FIGURES	ix
LIST OF APPENDICES	xi
ABSTRACT.	xii
INTRODUCTION	2
DESCRIPTION OF STUDY AREA	9
METHODS AND MATERIALS	20
DISTINGUISHING CHARACTERISTICS	25
LENGTH FREQUENCIES, GONADAL MATURITY, AND SPAWNING	26
FOOD HABITS.	35
INTRODUCTION	35
OVERALL FOOD HABITS FOR EACH SPECIES	36
MONTHLY COMPARISONS	41
SEASONAL COMPARISONS	51
SUMMARY OF FOOD HABITS	66
CURRENT PREFERENCES	73
MISCELLANEOUS HABITAT PREFERENCES	80
DISCUSSION	87
APPENDICES	105

	Page
LITERATURE CITED	109
VITA	118

ACKNOWLEDGMENTS

I thank Dr. Garnett R. Brooks, Jr., the chairman of my thesis committee, for his guidance during this study and his assistance in the field. I also thank the other members of my committee Drs. Gregory M. Capelli and Mitchell A. Byrd for guidance during my work and for reviewing my manuscript.

Special thanks go to Dr. Robert E. Jenkins of Virginia Commonwealth University who introduced me to this problem and gave me invaluable advice on the identification of Potomac drainage sculpins.

This work could not have been completed without the assistance of my wife Rebecca Lawrence Matheson who not only tolerated me during this period of time but was also my major assistant in the field and helped in the drawing of the figures.

Finally, several additional people provided assistance at various times during my work. David Reed, Dave Hartzband, Dr. R. J. Diaz, and Dr. M. A. Chmielewski provided statistical advice. George Van Dyke and Janet Goman assisted in locating specimens at the U.S. National Museum. Bland Crowder and Steve Hastings helped in the field on different occasions. Assistance in invertebrate identification was provided by Katie Kowalski, Marcia Bowen, and Dr. J. F. Matta. The manuscript was typed by Jane Kraft. In addition, Mike McCoid, George Sedberry, and

Dr. J. D. McEachran provided advice on various aspects of my work.

My support during this study was provided by the Biology Department of the College of William and Mary and by my wife.

LIST OF TABLES

Table	Page
1. Altitude, Distance from Mouth, Depth, and Width for Each Sampling Station	12
2. The Fishes of Naked Creek	15
3. The Invertebrates of Naked Creek	16
4. Size Ranges for Young-of-the-year <u>Cottus bairdi</u> and <u>Cottus girardi</u>	31
5. Overall Diet of <u>Cottus bairdi</u> and <u>Cottus girardi</u>	37
6. Mann-Whitney or Kruskal-Wallis Tests of the Signifi- cance of Differences in Numbers of Chironomid Larvae Eaten by <u>Cottus bairdi</u> and <u>Cottus girardi</u> . . .	44
7. Mann-Whitney or Kruskal-Wallis Tests of the Signifi- cance of Differences in Numbers of Copepods Eaten by <u>Cottus bairdi</u> and <u>Cottus girardi</u>	48
8. Mann-Whitney or Kruskal-Wallis Tests of the Signifi- cance of Differences in Numbers of Ephemeropteran Larvae Eaten by <u>Cottus bairdi</u> and <u>Cottus girardi</u>	49
9. Winter Diet Overlap between <u>Cottus bairdi</u> and <u>Cottus girardi</u>	54
10. Spring Diet Overlap between <u>Cottus bairdi</u> and <u>Cottus girardi</u>	59
11. Summer Diet Overlap between <u>Cottus bairdi</u> and <u>Cottus girardi</u>	63
12. Fall Diet Overlap between <u>Cottus bairdi</u> and <u>Cottus</u> <u>girardi</u>	67
13. Current preference Overlap and Chi Square Probabilities of the Absence of Difference in Current Preference for <u>Cottus bairdi</u> and <u>Cottus girardi</u> from Stations 2 through 6	77

Table	Page
14. Substrate Preference Overlap for <u>Cottus bairdi</u> and <u>Cottus girardi</u> from Stations 2 through 6.	83

LIST OF FIGURES

Figure	Page
1. Map of Lower Naked Creek	10
2. Length frequencies for both sexes of <u>Cottus bairdi</u> and <u>Cottus girardi</u>	27
3. Overall length frequencies by month for <u>Cottus bairdi</u> and <u>Cottus girardi</u>	28
4. Length frequencies for <u>Cottus bairdi</u> and <u>Cottus</u> <u>girardi</u> at Station 4 on August 27 and 28, 1977.	29
5. Mean diameter of largest ova by month for female <u>Cottus bairdi</u> and <u>Cottus girardi</u>	32
6. Mean number per stomach per month for several major food items in <u>Cottus bairdi</u> and <u>Cottus girardi</u>	42
7. Major winter foods of <u>Cottus bairdi</u> and <u>Cottus girardi</u> as percent frequency of occurrence, percent total number, and percent frequency of occurrence as dominant item	52
8. Major spring foods of <u>Cottus bairdi</u> and <u>Cottus girardi</u> as percent frequency of occurrence, percent total number, and percent frequency of occurrence as dominant item	56
9. Major summer foods of <u>Cottus bairdi</u> and <u>Cottus girardi</u> as percent frequency of occurrence, percent total number, and percent frequency of occurrence as dominant item	60
10. Major fall foods of <u>Cottus bairdi</u> and <u>Cottus girardi</u> as percent frequency of occurrence, percent total number, and percent frequency of occurrence as dominant item	64

Figure	Page
11. Percentages of <u>Cottus bairdi</u> and <u>Cottus girardi</u> found at various current speeds	74
12. Percentages of <u>Cottus bairdi</u> and <u>Cottus girardi</u> found on various substrate types	81
13. Percentages of <u>Cottus bairdi</u> and <u>Cottus girardi</u> found at various depths	84
14. Percentages of <u>Cottus bairdi</u> and <u>Cottus girardi</u> found at various distances from the nearest shore . . .	85

LIST OF APPENDICES

Appendix	Page
A. Details of Collecting Trips to Naked Creek	105
B. Sample Sizes Used in Mann-Whitney or Kruskal-Wallis Tests	108

ABSTRACT

The two sculpins, Cottus b. bairdi and Cottus girardi, coexist in Naked Creek, Virginia. The purpose of this study was to compare the use of available resources by these two fish. Major emphasis was directed at food habits and habitat preferences; spawning and size differences were also examined.

The diets of these two species were quite similar but differences did exist in the importance of several food items. Diets were compared among six fish groups (males, females, and immatures of both species) and differences were analyzed on the basis of fish size, fish habitat preferences, and prey habitat preferences.

These same six fish groups were also compared in the analysis of habitat preferences. The habitat was most obviously divided on the basis of current speed. A faster current group consisted of female and immature C. bairdi, while a slower or no current group consisted of male and immature C. girardi. Female C. girardi approached the former group in current preferences, and male C. bairdi approached the latter group. Further habitat segregation was seen in preferred substrate type, depth, and distance from shore.

Cottus girardi was larger during its first summer of life than was C. bairdi and may reach a larger maximum size. Also, female C. girardi matured at a larger size.

Cottus bairdi spawned under rocks in current during March and April, but no C. girardi nests were found. Based on the size differential among young and the literature concerning the closest relatives of C. girardi, it was postulated that C. girardi probably spawned earlier than C. bairdi and probably utilized a different spawning habitat.

INTRODUCTION

Fishes of the circumpolar genus Cottus are often confusingly similar in terms of both systematics and ecology. The systematic complexity of this genus is perhaps best stated by Bailey and Dimick (1949): "Of all North American fresh-water fishes, probably no group is of more potential significance to the evolutionist than is the genus Cottus. Among its many forms convergent and divergent evolution is rife, geographic variation is often extreme, and individual variation may be great. The parallel evolution of almost all characters in diverse phyletic lines renders difficult the recognition of natural affinities. Cottus appears to be a plastic group, and in attempting to fit morphological variants into an orderly arrangement the systematist repeatedly experiences frustration." Schultz (1930) finds variation in Washington sculpins to be so great between streams and within streams, that he concludes that many characters used by taxonomists are probably invalid. Robins (1954) comments that the identification of various species is complicated by excessive variation within species. This variation often exceeds and masks the differences between species when entire ranges are considered. Robins (1961) also mentions that it is typical of Cottus that a C. bairdi subspecies living sympatrically with C. baileyi is more divergent from C. bairdi (in other parts of its range) in many characters than is C. baileyi (the subspecies can be connected to C. bairdi by intergrading populations). As one might expect, the existence

of such complex interrelationships within a group of organisms has stimulated the publication of much systematic literature. Most of that up to 1954 is reviewed by Robins (1954), and Strauss (1977) mentions many of the more recent papers.

In addition to their confusing degree of morphological similarity, most Cottus species also have similar life styles. They are usually benthic fishes of fresh-water lakes and streams. They are predators: most of them consume benthic invertebrates or small fish (Scott and Crossman 1973; Hubbs and Lagler 1958; Eddy 1969).

Robins (1954, 1961) described a new member of the Cottus carolinae group as Cottus girardi (the Potomac sculpin) and considered it to be endemic to the Potomac River drainage. One or perhaps two members of the Cottus bairdi or "redfin" group, Cottus b. bairdi (the northern mottled sculpin) and a form related to C. cognatus (the slimy sculpin), also occur in the Potomac drainage.

Savage (1962) places C. bairdi and C. girardi in synonymy based on behavioral evidence plus a reexamination of the characters used by Robins in separating the two fish. Furthermore, one of these characters, the union of the preoperculomandibular canals in C. girardi, is considered to be a common character in C. bairdi by Bailey and Bond (1963).

Several authorities, however, do not accept this synonymy. R. E. Jenkins and B. B. Collette (pers. comm.) agree with Robins' contention that C. girardi is a valid species. Franz and Lee (1976) also discuss this problem and Lee et al. (1976) (in unpublished addenda) make the following comment: "As a result of further study, we are now completely convinced

that the Potomac sculpin, Cottus girardi Robins, is a valid species."

Recently, two workers, Strauss (1977, unpublished thesis) and Matthews (unpublished manuscript), have completed systematic studies of C. bairdi and C. girardi. On the basis of both biochemical and morphological evidence both of them believe that C. girardi is a valid species. Thus, the Potomac River drainage contains at least two ecologically similar sculpins which might be considered potential competitors.

The literature contains records of at least 15 species in this genus occurring sympatrically with one or more congeners (Bailey and Bond 1963; Cihar 1969; Robins and Miller 1957; Crawford 1927; Hubbs 1920; Robins 1954; Pasch and Lyford 1972), and this list is doubtless incomplete. Bailey and Bond (1963) report that C. confusus can be found living with C. bairdi, C. cognatus, C. beldingi, C. rhotheus, C. asper, or C. aleuticus. In fact, C. confusus plus the latter three species were all taken from one river in Washington. The ecological overlap in these situations varies from almost complete segregation to apparently complete integration. Thus, the members of this genus make excellent subjects for studies of competition, resource partitioning, and related subjects.

The formulation of the idea of competitive exclusion is often attributed to Gause (1934) but, as Harper et al. (1961) indicate, Darwin [1859 (seen in 1886 edition)] (among others) had conceived of the idea much earlier. A shortened version of Hardin's (1960) statement of this principle would read as follows: if two species occupy exactly the same niche, are sympatric, and do not multiply at exactly the same rate, then the one multiplying at the slower rate will eventually be replaced by its neighbor

and become extinct. Since the last condition would seldom be met in nature and since the "compound interest" effect of Hardin (1960) should make extinction a fairly rapid event, the species that one finds coexisting today (excluding those environments recently altered by man) should not be occupying exactly the same niche. Thus, if two forms are not members of the same gene pool, then they must be partitioning the available resources in some manner (excluding the unlikely possibility that the quantity of all resources is unlimited). Ecological evidence on the overlap in resource use between sympatric congeners can, therefore, be of use to the systematist (Kohn and Orians 1962).

This concept is not, however, accepted by all ecological theorists as a useful framework for the study of comparative ecology (Birch and Ehrlich 1967). These authors stress the circular nature of explaining present resource partitioning on the basis of past competition and then referring to this resource partitioning as proof of the existence of past competition. Nevertheless, despite the fact that the competitive exclusion principle may not be subject to rigorous proof, closely related species living in the same area do tend to partition the available resources (Kohn and Orians 1962).

Many equations for calculating the degree of overlap in resource use between species are presented in the literature (Horn 1966; Colwell and Futuyama 1971; Sale 1974; Hurlbert 1978). As the latter two authors indicate, however, these indices can only measure overlap in resource use and not competition (unless the variation in abundance of needed resources is taken into account). This fact, nevertheless, does not negate the

usefulness of such measures in studies designed only to demonstrate the presence or absence of resource partitioning.

Many researchers have published studies of competition and resource partitioning. Schoener (1974) reviews and gives examples of these works. Such studies involve a wide range of organisms, and several recent ones deal with fishes (e.g., Zaret and Rand 1971; Werner 1977; Werner and Hall 1976; Werner et al. 1977; Ross 1977; Mendelson 1975; McEachran and Martin 1977; Keast 1977; Nursall 1974; Gibbons and Gee 1972).

Most studies on the genus Cottus, however, have not dealt directly with this problem. Many studies, such as those of Ebert and Summerfelt (1969) and Craig and Wells (1976), concern food habits or other aspects of the ecology of single species. Those studies which do compare resource use in sympatric sculpins include Mason and Machidori (1976) (Cottus aleuticus and C. asper in British Columbia), Pasch and Lyford (1972) (C. perplexus and C. rhotheus in Oregon), and Northcote (1954) (C. asper and C. rhotheus in British Columbia). Perhaps the most extensive studies, however, are those of Andreasson (1968, 1969a, 1969b, 1972a, 1972b, 1973), Starmach (1962, 1970, 1971, 1972), and Cihar (1969) which compare the ecologies of C. gobio and C. poecilopus in Europe.

As mentioned by Robins (1961) the uncertainty of the taxonomic situation makes it impossible to allocate previous references on Potomac drainage sculpins to any one species. Therefore, very little ecological data are available for C. girardi. Robins (1954, 1961) states that the Potomac sculpin occurs with C. bairdi in "clear water riffles." He does mention, however, that C. girardi is generally more tolerant of warmer

downstream conditions than is C. bairdi. Savage (1963) notices no differences in breeding between the two species, but there is some doubt about the identify of his specimens (Jenkins pers. comm.; Matheson pers. obs.). Strauss (1977) cites differences in the width of the vomerine tooth patch, the length of the premaxilla, and the length of the head as possible evidence of resource partitioning in terms of food utilization. He also notes that greater pectoral fin area in C. girardi and the larger number of lateral line pores and deeper caudal peduncle in C. bairdi may be related to differences in microhabitat. Matthews (pers. comm.) notices a tendency for C. bairdi to occur in riffles, while C. girardi is more common in deeper areas below riffles.

The ecological requirements of Cottus carolinae, C. girardi's closest relative, may or may not be similar to those of C. girardi. The few references on the ecology of C. carolinae (e.g., Craddock 1965; Minckley 1963; Minckley et al. 1963; Small 1975; Robins 1961; Williams and Robins 1970; Blankenship and Resh 1971) may, therefore, be of interest in this study.

References do exist on the ecology and life history of C. bairdi populations in many different areas (excluding the Potomac drainage). Such studies in the eastern United States include Fish (1932) in Lake Erie, Koster (1937) and Daiber (1956) in New York, Turner (1922) and Downhower and Brown (1977) in Ohio, Coffman et al. (1971) and Walker (1975) in Pennsylvania, Burton and Odum (1945) in Virginia, and Addair (1945) in West Virginia. In the central United States C. bairdi has been studied by Anderson and Smith (1971) in Lake Superior; Anderson (1975)

in Illinois; Reighard (1915), Smith (1922), Hann (1927), Greeley (1932), and Manion (1977) in Michigan; Surber (1920, cited by Bailey 1952) and Dineen (1951) in Minnesota; and Pearse (1918), Ludwig and Norden (1969) and Ludwig and Lange (1975) in Wisconsin. In the western United States this species has been studied by Bailey (1952) and McCleave (1964) in Montana, Bond (1963) in Oregon, Zarbock (1952) in Utah, Patten (1971) in Washington, and Simon and Brown (1943) in Wyoming. In addition, Hallam (1959) and Emery (1973) discuss this species in Ontario.

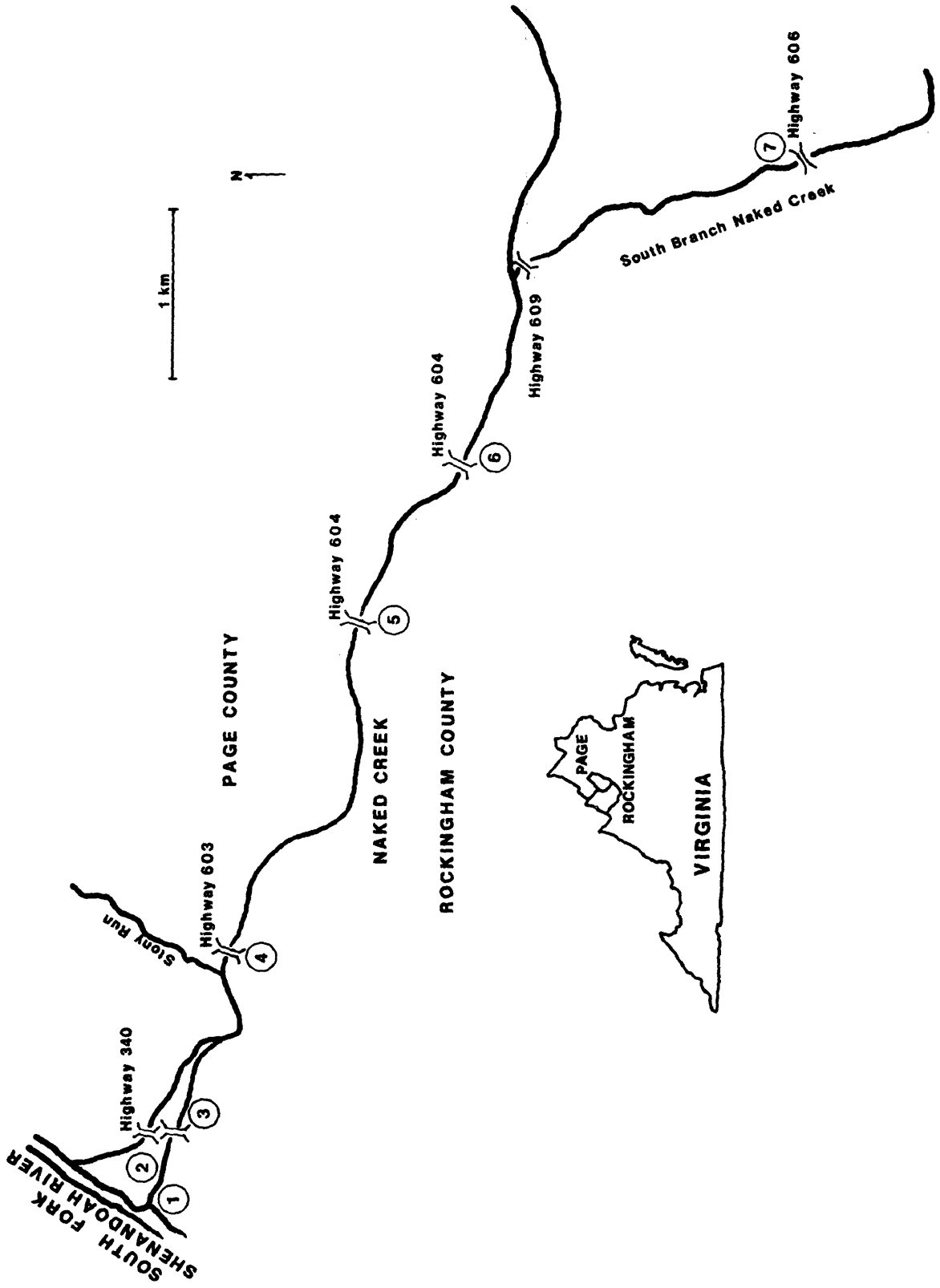
The purpose of the present research is to compare the use of environmental resources by Cottus girardi and C. b. bairdi in Naked Creek, Virginia. The resources of food and living space will be emphasized. Notes will also be presented on those characters which proved most useful in the separation of these two species.

DESCRIPTION OF STUDY AREA

Naked Creek forms a portion of the border between Page and Rockingham counties in north-central Virginia (Fig. 1). It originates in the Shenandoah National Park on the western slope of the Blue Ridge Mountains and flows into the South Fork of the Shenandoah River which is part of the Potomac River drainage. The water has the clarity that is typical of the rocky substrate streams in this mountainous area, and aquatic life is abundant. This picturesque stream is not, however, untouched by humanity. In the area covered by this study the surrounding countryside is generally pasture and farmland with a few scattered homes and small stores along the creek bank. At least some of these homes and stores have outdoor toilets which are located quite close to the stream. Therefore, one could assume that agricultural runoff and outhouse seepage enter the stream on occasion. These substances could be contributing factors in the excessive growth of filamentous algae during the warmer months. Large amounts of garbage in the form of cans, bottles, cardboard, paper, and other items are also present in the stream, especially in the vicinity of bridges which cross the creek. In addition, many areas of the stream have been channelized.

Cady (1936) describes the geology of the area surrounding Naked Creek. The stream originates in Precambrian crystalline rocks and flows through Cambrian sandstones, shale, dolomite, quartzite, and limestone.

Fig. 1. Map of lower Naked Creek, Virginia (adapted from Elkton East Quadrangle, Virginia. U.S. Dept. of Interior, Geol. Survey, 1972: 7.5 Minute Series). Circled numbers indicate the location of stations described in Table 1 and in text.



According to Harris (1972) a sample from an outcrop of the Erwin Formation along Naked Creek had the following chemical composition: SiO_2 - 99.3%, Al_2O_3 - 0.3%, Fe_2O_3 - 0.59%, Ca - 0.01%, MgO - 0.01%, K_2O - 0.7%, and Na_2O - 0.03%.

Fig. 1 is a map of the section of Naked Creek covered by this study. Sampling was generally limited to a 30 to 60 m section of stream at each station. Stations 1 through 6 are located within a fourth order stream segment whereas Station 7 is in a third order segment (as defined by Strahler 1954, 1957 in Beaumont 1975). Table 1 gives the altitude, the distance from the creek mouth, sampling depths, and stream widths for each station. The stream gradient averages 9.8 m/km over the sampling area.

Flow volume and water temperature changed considerably during the study. In the low water period of August 1976, Station 7 was reduced to one pool of approximately 40 m^2 with dry stream bed occurring both up- and downstream. Flow volumes at Station 5 (measured by the method of Davis 1938 in Hynes 1970) varied from $0.05 \text{ m}^3/\text{s}$ in September 1976 to $1.67 \text{ m}^3/\text{sec}$ in November 1976. Water temperatures ranged from 0 C in February 1977 (when much of the stream was covered by ice) to 27.2 C in July 1976. Daily temperature variations were as great as 6 C at one station. Also, there was generally a temperature difference of a few degrees between the mouth and the upstream stations.

A variety of current and substrate types are present at most stations. Usually these range from moderate- or fast-flowing riffles with clean cobble and boulder substrates to slow-flowing or dead areas with

TABLE 1

ALTITUDE, DISTANCE FROM STREAM MOUTH, SAMPLING DEPTHS, AND
STREAM WIDTHS FOR SAMPLING STATIONS.

Station	Altitude (m above sea level)	Distance from mouth (km)	Sampling depth range (cm)	Stream width range (m)*
1	274	0	15-40	4-8
2	274	0.3	13-24	18
3	280	0.5	10-40	--
4	287	1.6	4-50	5-30
5	305	3.8	3-50	8-18
6	314	5.4	3-100	10-14
7	354	8.2	4-65	5-16

*Measured at the exact locations of individual samples.

accumulations of silt and debris. The former is usually dominant in terms of stream area. One notable exception to this rule is Station 2. This is a moderate to slow, wide, flatwater section of stream. Sampling at this station, however, was confined to a narrow strip along the north bank. This strip was occupied by a large bed of Elodea sp. in warm weather.

The type of shoreline also varies from station to station. At Station 1 the south bank consists of a small delta with low herbaceous vegetation at the mouth and a mud cliff backed by deciduous trees a little farther upstream. Behind these trees is an abandoned farm which extends upstream to Station 2. The north shore at Station 1 is a beach-like floodplain with herbaceous vegetation and small willows and sycamores. At Station 2 the south shore is lined with tall, overhanging trees and the north shore is a small, steep bank covered with low vegetation and backed by a pasture. Both banks at Station 3 are high, steep, and strewn with boulders. Low shrubs and weeds occur among these rocks. The south bank at Station 4 is a gentle slope with a few scattered boulders and herbaceous vegetation. The north bank is steeper with herbaceous vegetation growing to the waterline backed by a row of tall trees and a few homes. Both banks at Station 5 are fairly similar to those at Station 4 with the exception that pastures and the remains of a burned-out store are just behind the creek bank. At Stations 6 and 7 the stream is channeled through pipes built into concrete bridges (these could be a considerable barrier to fish movement when the water level falls below the downstream mouth of the pipes). Both banks at Station 6 consist of rocks mixed with herbaceous growth.

Open fields are behind the stream banks on the north shore, and a house trailer on cleared land occupies the area on the south shore upstream from the bridge. The stream is heavily shaded by overhanging trees on the upstream side of the bridge at Station 7. Below the bridge the south shore consists of weeds and a few trees backed by a small field and an abandoned home. The north shore is a rocky, weeded bank between the creek and the road.

In the warmer months aquatic and semi-aquatic plants form a major habitat type. Thick beds of filamentous algae are present at most stations in the summer and at some stations even in the winter. Encrusting algae is present throughout the year on most surfaces that are exposed to sunlight. Elodea sp. occurs at Stations 2 and 4 and Potamogeton sp. occurs at Station 4. Emergent semi-aquatic plants are prominent at Stations 1 and 4.

Tables 2 and 3 list the fishes and invertebrates of Naked Creek. I should point out that fish collecting methods were aimed at small, slow benthic fishes and, therefore, groups such as the centrachids, salmonids, and catostomids are probably underrepresented in my collections. Nevertheless, obvious changes take place in the fish community as one proceeds from the mouth to Station 7. The invertebrate samples were random and non-quantitative.

TABLE 2
FISHES COLLECTED AT EACH STATION*

Species	Stations:	1	2	3	4	5	6	7
<u>Rhinichthys atratulus</u>		x	x	x	x	x	x	x
<u>Cottus bairdi</u>		x	x	x	x	x	x	x
<u>Cottus girardi</u>		x	x	x	x	x	x	x
<u>Etheostoma flabellare</u>		x	x	x	x	x	x	x
<u>Rhinichthys cataractae</u>		x		x	x	x	x	x
<u>Ictalurus natalis</u>		x	x					
<u>Catostomus commersoni</u>			x					
<u>Noturus sp.</u>			x					
<u>Lepomis macrochirus</u>			x					
<u>Micropterus salmoides</u>			x					
<u>Exoglossum maxilingua</u>			x		x	x		
<u>Pimephales notatus</u>			x		x			
<u>Ambloplites rupestris</u>			x		x			
<u>Notropis spilopterus</u>					x			
<u>Semotilus corporalis</u>					x			
<u>Micropterus dolomieu</u>					x	x		
<u>Nocomis leptocephalus</u>					x	x		x
<u>Hypentilium nigricans</u>						x		
<u>Notropis cornutus</u>						x	x	
<u>Clinostomus funduloides</u>							x	x
<u>Chrosomus oreas</u>								x
Unidentified young salmonid								x

*Identifications of all species (with the exception of the two sculpins) are based on keys found in Blair et al. (1957), Eddy (1969), and Loos et al. (1972).

TABLE 3

NAKED CREEK INVERTEBRATES
 (*denotes groups included in the diet of sculpins)

Cnidaria (Coelenterata)	Mandibulata
Hydrozoa	Crustacea
<u>Hydra</u> sp.*	Branchiopoda
Platyhelminthes	Cladocera
Turbellaria	Chydoridae*
Tricladida	Ostracoda*
Planariidae*	Copepoda
<u>Cura foremanii</u> ?	Cyclopoida*
<u>Phagocata</u> sp.	Malacostraca
Nematoda*	Amphipoda*
Mollusca	Decapoda
Gastropoda	Astacidae
Ctenobranchiata	Cambarinae*
Viviparidae	<u>Orconectes</u> (<u>Orconectes</u>) sp.
<u>Lioplax</u> sp.*	Insecta
<u>Viviparus</u> sp.	Coleoptera
Pulmonata	Adephaga
Lymnaeidae	Dytiscidae
<u>Lymnaea</u> sp.	Hydroporinae*
Physidae	Haliplidae
<u>Physa</u> sp.*	<u>Peltodytes</u> sp.*
Planorbidae	Gyrinidae
<u>Helisoma</u> sp.*	<u>Dineutus</u> sp.*
Annelida	Polyphaga
Hirudinea	Chrysomelidae*
Oligochaeta	Elmidae
Plesiopora*	Hydrophilidae*
Prosopora*	<u>Cymbiodyta</u> sp.
Lumbriculidae	Dryopidae
Arthropoda	<u>Helichus</u> sp.*
Chelicerata	Diptera
Arachnida	Nematocera
Acari*	

TABLE 3 (Continued)

Simulidae*	Siphonuridae
Chironomidae	<u>Isonychia</u> sp.*
Tanypodinae	<u>Ameletus</u> sp.*
<u>Pentaneura</u> sp.*	<u>Siphonurus</u> sp.*
Pelonae*	Tricorythidae
Tipulidae	<u>Tricorythodes</u> sp.*
<u>Antocha</u> sp.*	Hemiptera
<u>Tipula</u> sp.*	Belostomatidae
Ceratopogonidae	<u>Belostoma</u> sp.
Heleinae*	Megaloptera
Brachycera	Corydalidae
Dolichopodidae*	<u>Corydalis</u> sp.
Empididae	Sialidae
<u>Roederoides</u> sp.*	<u>Sialis</u> sp.*
Muscidae*	Odonata
Rhagionidae	Anisoptera
<u>Atherix variegata</u>	Aeshnidae
Ephemeroptera	<u>Basiaeschna janata</u>
Neophmeridae	Gomphidae
<u>Neophmera</u> sp.	<u>Dromogomphus spoliatus</u> *
Baetidae	<u>Lanthus albistylus</u>
<u>Centroptilum</u> or <u>Cloeon</u> sp.?	Zygoptera
<u>Pseudocloeon</u> sp.*	Coenagrionidae*
Caenidae	Plecoptera
<u>Caenis</u> sp.*	Filipalpia
Ephemerellidae	Nemouridae
<u>Ephemerella</u> (<u>Ephemerella</u>) sp.*	<u>Nemoura</u> sp.
<u>Ephemerella</u> (<u>Drunella</u>) sp.*	Capniidae
<u>Ephemerella</u> (<u>Seratella</u>) sp.*	<u>Allocapnia</u> sp.*
Heptageniidae	Pteronarcidae
<u>Epeorus</u> (<u>Iron</u>) sp.*	<u>Pteronarcys</u> sp.*
<u>Stenonema</u> sp.*	Taeniopterygidae
<u>Stenacron</u> sp.*	<u>Taeniopteryx</u> sp.
Leptophlebiidae	Setipalpia
<u>Paraleptophlebia</u> sp.*	Perlidae
Polymitarcidae	<u>Acroneuria</u> sp.*
<u>Ephoron leukon</u>	<u>Perlesta</u> sp.*
Potamanthidae	
<u>Potamanthus</u> sp.*	
Ephemeridae	
<u>Hexagenia</u> (<u>Hexagenia</u>) sp.	

TABLE 3 (Continued)

Tricoptera

Glossosomatidae

Glossosoma sp.*

Hydropsychidae

Cheumatopsyche sp.*Hydropsyche sp.*

Hydroptilidae

Agraylea sp.*Hydroptila sp.*Oxyethira sp.*

Leptoceridae

Mystacides? sp.Oecetus sp.Setodes sp.*

Lepidostomatidae*

Odontoceridae

Psilotreta sp.*

Limnephilidae

Neophylax sp.Pycnopsyche sp.

Polycentropodidae

Polycentropus sp.*

METHODS AND MATERIALS

Details of each collecting trip are presented in Appendix A. Collections were made in every month except December and January. Some months are represented by more than one collecting trip during the same or different years. Sampling effort was concentrated at Stations 4 and 5 due to the abundance of sculpins and the variety of habitat types at these two stations. Other stations were sampled as time permitted. An effort was made to distribute samples over a wide variety of habitat types on each collecting trip.

Three capture methods were employed during this study. Equipment included a 2 m seine with 6 mm mesh, a 0.5 m seine with 2 mm mesh, and various small, short-handled dip nets (aquarium nets). The seines were used in areas with current and areas with large beds of aquatic plants (Elodea sp.). In current, one person held the seine in place while another person vigorously turned stones and disturbed the substrate just upstream. The area thus sampled was approximately 1 m^2 . In beds of aquatic plants the seine was forced partially underneath the vegetation which was then shaken vigorously. The larger seine was used for most collections but the smaller one was used during late spring and early summer due to the small size of young-of-the-year fish. Seining proved ineffective, however, in areas with little or no current. The dip nets were used in these areas. Capture of individual sculpins by this method

proved tedious, but most fish, once located, could be forced into the net either by one's hand or by another dip net. Larger fish were easier to see but somewhat harder to catch than smaller fish. A diving mask was useful in deeper areas for this type of sampling, and a wet suit was required in colder months.

Current or current type, substrate type, depth, temperature, and distance from the nearest shore were recorded for most individual samples. These measurements were sometimes omitted when it was necessary to obtain larger samples for food habits analysis. Current speed was estimated by recording the amount of time required for a floating object to travel over a measured distance. When such measurement was impractical stream flow was classified as either current, eddy, or dead. Substrate was classified according to its dominant component in a particular sampling area. Categories included boulder, cobble, pebble, sand-and-gravel, silt, and vegetation. The first four of these are clean stone substrates with size ranges as in Hynes (1970). An area was considered silty if all surfaces were covered with a thick layer of material which was readily suspended in the water column by minor agitation. The vegetation category included areas dominated by floating or attached mats of algae and those dominated by beds of aquatic macrophytes.

In addition to the above data, brief observations were made in regard to spawning.

All fish were preserved immediately in 10% formalin and later transferred to 70% ethanol. Standard length (SL), alcohol weight, and various diagnostic characters were recorded for each fish. Food items were

removed from the entire digestive tract anterior to the pylorus (including the oral cavity). These items were then identified to the lowest practical taxonomic level. Keys found in Borror and DeLong (1971), Edmunds et al. (1976), Frison (1935), Needham and Westfall (1955), Pennak (1978), Usinger (1956), Ward and Whipple (1959), and Wiggins (1977) were used in these identifications. Numbers in each of the various taxa were recorded along with the individual taxon which seemed to comprise the bulk (by volume) of the stomach contents. Gonads were examined to determine sex, and the maximum ova diameters were recorded for each ovary.

Sculpin identification was based on a combination of characters. Jenkins (pers. comm.) separates Cottus girardi from C. bairdi mainly on the basis of chin pigmentation and the nature of the side bands (saddles). In C. girardi the chin is moderately to considerably mottled while in C. bairdi pigment is uniformly distributed over the chin. Also, the saddles of C. girardi tend to become distinctly narrower at the dorsum while those of C. bairdi do not decrease appreciably in width. Matthews (unpubl.) obtains 100% agreement between identification of fish by the nature of the chin and saddles and that by electrophoresis. Collette (pers. comm.) agrees that these two species are easily separated in Conococheague Creek, Pennsylvania [the type locality for C. girardi (Robins 1954, 1961) and the origin of Matthew's specimens], but Strauss (pers. comm.) indicates that identification is more difficult in other areas. My identifications were based on a combination of the above mentioned characters plus two other characters which I have found useful (see below). After

looking at large numbers of specimens, I had little difficulty in separating Naked Creek sculpins into two distinct groups.

No definite C. cognatus were collected in Naked Creek. Four specimens were, however, eliminated from the ecological study due to uncertain identification. One of these fish appears to be intermediate in several characters between C. bairdi and C. girardi. Two specimens possess the squarish blotches on the lower sides which Jenkins (pers. comm.) attributes to Potomac drainage C. cognatus. The remaining fish is melanistic with the excess of pigment concealing all other characters (this is not a breeding male but is a very young fish with black pigment over most of its body). No C. bairdi used in this study possess the three pelvic rays on each side that are characteristic of C. cognatus (Jenkins pers. comm.; Strauss 1977) Six specimens do, however, have three pelvic rays on one side and four on the other. One aberrant specimen also has two pelvic rays on one side and three on the other.

For comparative purposes each species was divided into mature males, mature females, and immatures. The point of separation between mature and immature fish was based on the results of other studies plus length frequencies and ovary development in Naked Creek specimens (see below). When necessary, intraspecific size and/or sexual groups were combined to give adequate sample sizes. Age determinations were not attempted except for inferences based on length frequency distributions.

Variability due to seasonal, temporal, spatial, and other differences between samples was controlled as much as possible by comparing

interspecific groups with similar capture data or by first testing for intraspecific differences to determine whether or not groups could be combined. Sample size was the main factor limiting this type of approach. For seasonal comparisons, February was considered winter, March through May were considered spring, June through August were considered summer, and September through November were considered fall.

Descriptive statistics used in comparing food habits include percent frequency of occurrence ("occurrence method" of Hynes 1950), percent frequency of occurrence as the dominant food item by volume (similar to the "dominance method" of Hynes 1950), percent of the total number of food items ("number method" of Hynes 1950), and mean number per stomach. Empty stomachs were eliminated from the calculation of all of these statistics. Further details on the method of comparing food habits will be presented in the introduction to the food habits section below.

Several statistical tests were used to determine the significance of observed trends in the data: Student's t-tests (Sokal and Rohlf 1969) were used for SL comparisons, Mann-Whitney U tests and Kruskal-Wallis one-way analyses of variance (Siegel 1956) were used for monthly food habits comparisons, and chi square tests of independence and Spearman's coefficient of rank correlation (Sokal and Rohlf 1969) were used for current preference comparisons. Some statistics were calculated by hand while others were calculated by computer using the programs available in the Statistical Package for the Social Sciences (Nie et al. 1975). In all tests probabilities of less than or equal to 0.05 were considered significant.

Finally, overlap values were calculated for food habits, and current and substrate preference data. The following index (Schoener 1968) was used:

$$D = 1 - 0.5 \sum_{i=1}^n |p_{x,i} - p_{y,i}|$$

where $p_{x,i}$ and $p_{y,i}$ are the frequencies of species x and y, respectively, in the i^{th} category. The value of this index ranges from 1 (for complete overlap) to 0 (for no overlap). For current data the range of current speeds in a given category was increased until the frequency of either of the two groups being compared exceeded 0.10. Related taxa (i.e., insects in the same order) were combined to reach this frequency in food habits comparisons, but no such combination seemed advisable in substrate comparisons. As a rule-of-thumb, overlap values greater than 0.60 were considered significant following the practice of Zaret and Rand (1971). Measurements of depth and distance from shore were too inaccurate and variable within a given sampling area for overlap values to be meaningful.

DISTINGUISHING CHARACTERISTICS

Two characters which proved very useful in separating Naked Creek fish are fin color and the nature of the band at the base of the caudal fin. In C. bairdi the second dorsal, caudal, and sometimes pectoral fins are normally red (ranging from red-brown to red-orange to nearly pink). These same fins in C. girardi are almost colorless or pale yellow. Out of 354 sculpins with uniform, C. bairdi-type chins, 95% had red fins, 2% had yellow fins, and 3% were breeding males with darkened fins. All of the 152 mottled chinned sculpins examined had colorless or yellow fins. This character is, however, only useful in fresh specimens due to the rapid fading of red pigment in ethanol.

The posterior, lateral margin of the band at the base of the caudal fin in C. girardi possesses a distinct V- or U-shaped notch while that in C. bairdi is more or less straight. Out of 424 C. bairdi examined, 92% had no notch on either side of the caudal peduncle, 6% had a notch on one side, and 3% had a notch on both sides. Out of 172 C. girardi, however, 99% had the notch on both sides and 1% had it on one side. I might also point out that, even in those specimens of C. bairdi which did possess this notch, its form was not as regular and it was not as pronounced as in C. girardi. Jenkins (pers. comm.) confirms the validity of this character in Potomac material from locations other than Naked Creek.

LENGTH FREQUENCIES, GONADAL MATURITY, AND SPAWNING

Comparison of length frequency data for males and females of both species (Fig. 2) indicates a possible sexual size difference in C. bairdi but no obvious difference in C. girardi. The sex of young-of-the-year fish was evident by June. At this time little size difference seemed apparent between the sexes in C. bairdi. By the following April-May, however, males appeared to be larger than females (modes 45-50 and 40-45 mm, respectively). Furthermore, this seemed to be the general trend in all months for older size groups. No such sexual size difference was obvious in the lengths of C. girardi (the sample sizes may have been too small to show a difference if it existed).

The largest samples (with both sexes combined) of older C. girardi are found in May, June, and August (Fig. 3). In the latter two months the modes for C. girardi were 5 mm higher than those for C. bairdi, and the entire distribution for C. girardi was relatively higher. Also, out of 28 fish greater than 60 mm (SL), 19 were C. girardi and 9 were C. bairdi. This same trend was evident in length frequencies for the largest sample that I have for one station in one year, Station 4 on August 27 and 28, 1977 (Fig. 4).

Young of both species first appeared in May (Fig. 3). Through at least August, young C. girardi were consistently larger than young C. bairdi (modes ranged from 5 to 10 mm higher and the distribution was

Fig. 2. Length frequencies for both sexes of Cottus bairdi and Cottus girardi. Data from all stations and all dates are combined for each two-month period. Numbers in parentheses are sample sizes (m = male and f = female).

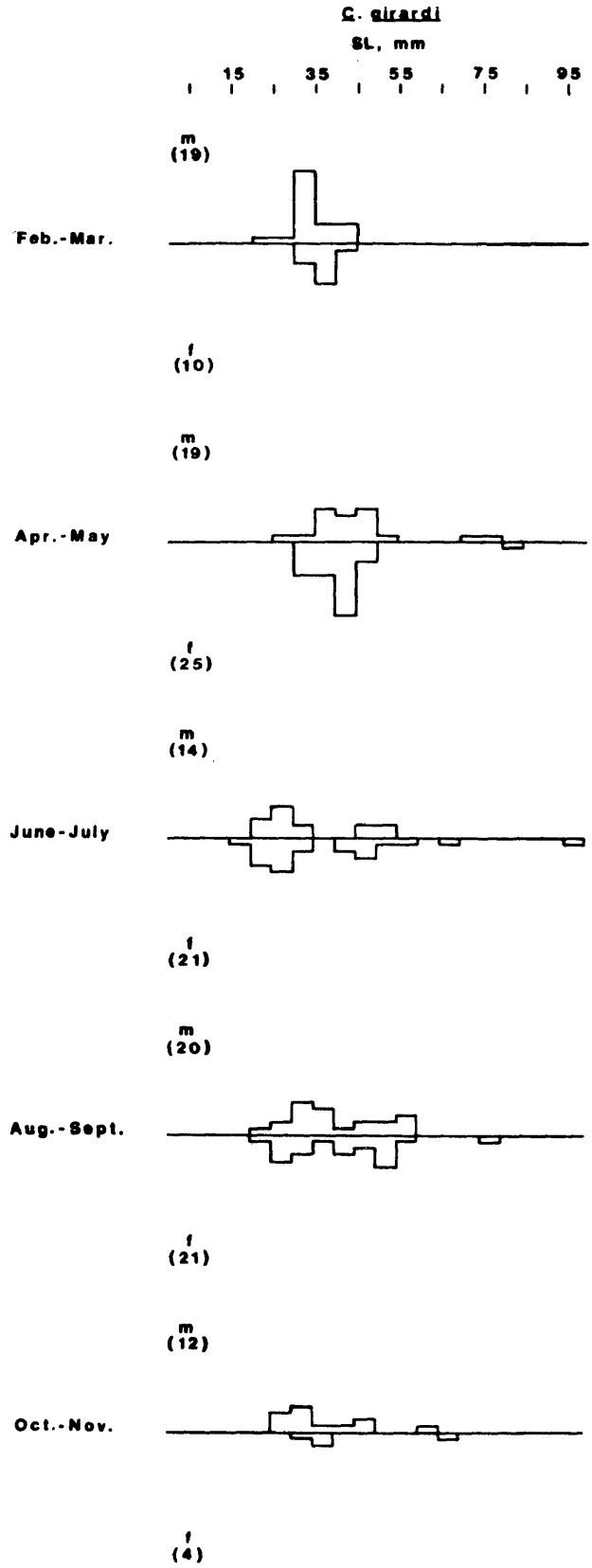
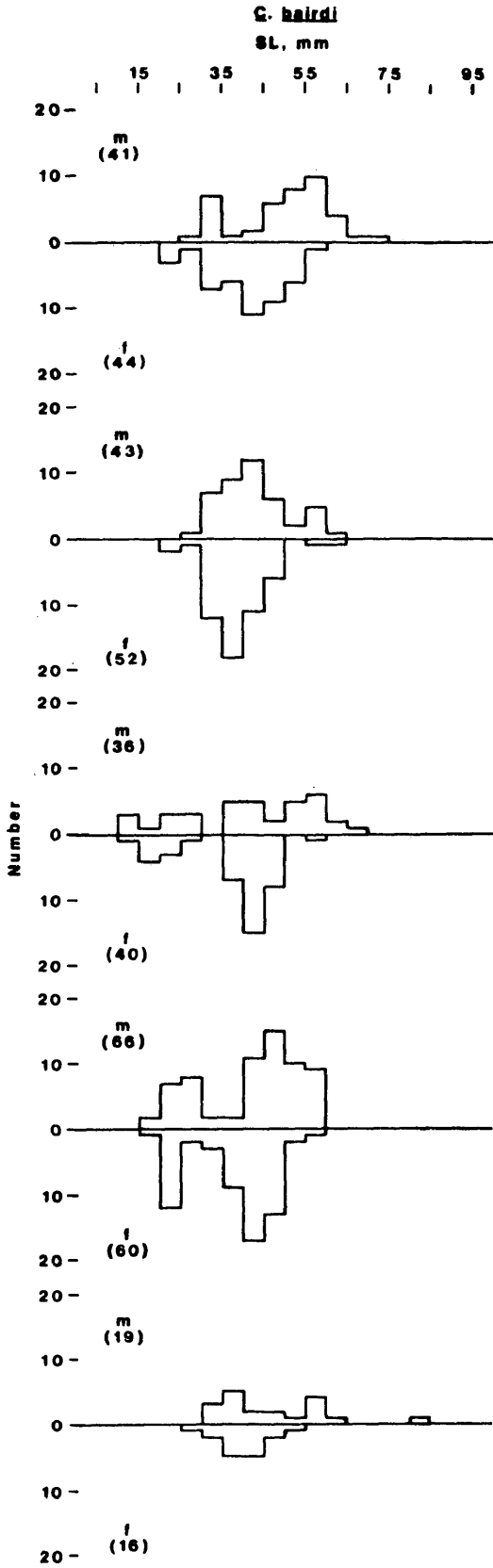


Fig. 3. Overall length frequencies by month for Cottus bairdi and Cottus girardi. Data from all stations and all dates are combined for each month. Open bars indicate C. bairdi and shaded bars indicate C. girardi. Numbers in parentheses are sample sizes.

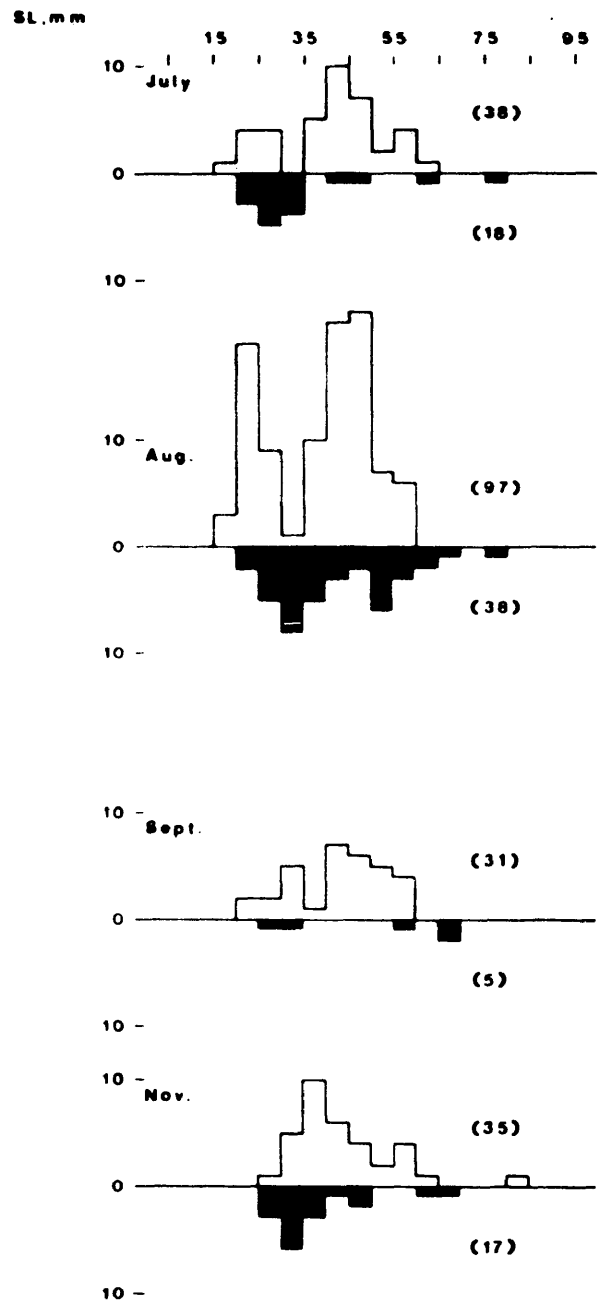
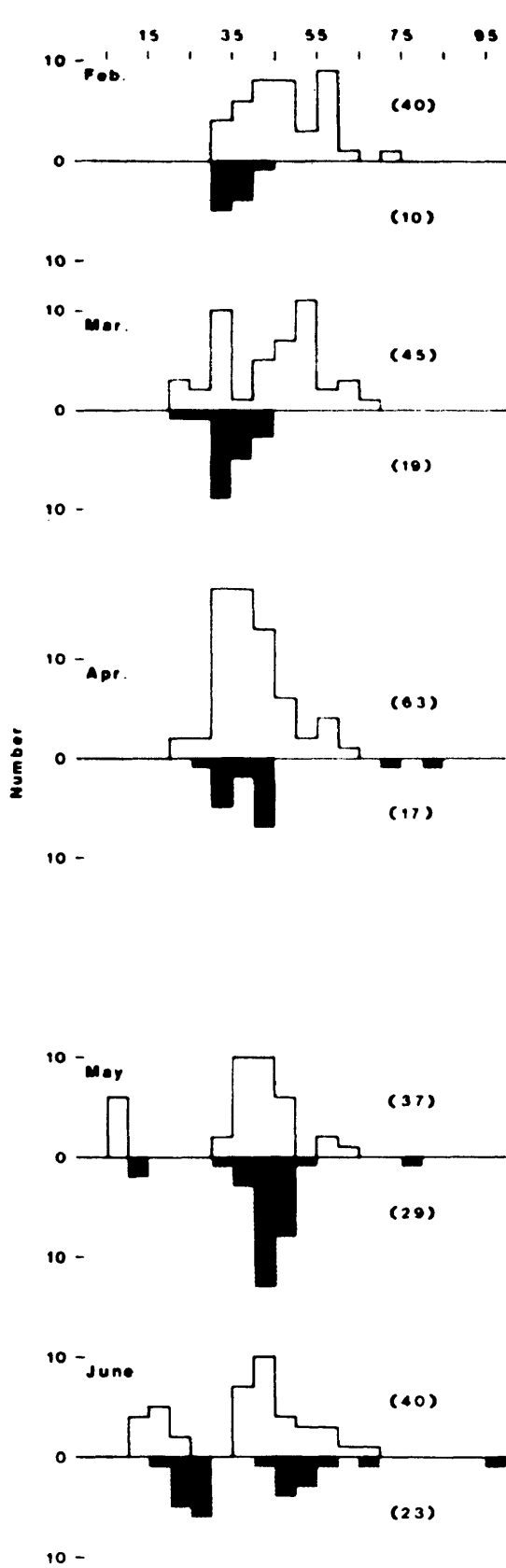
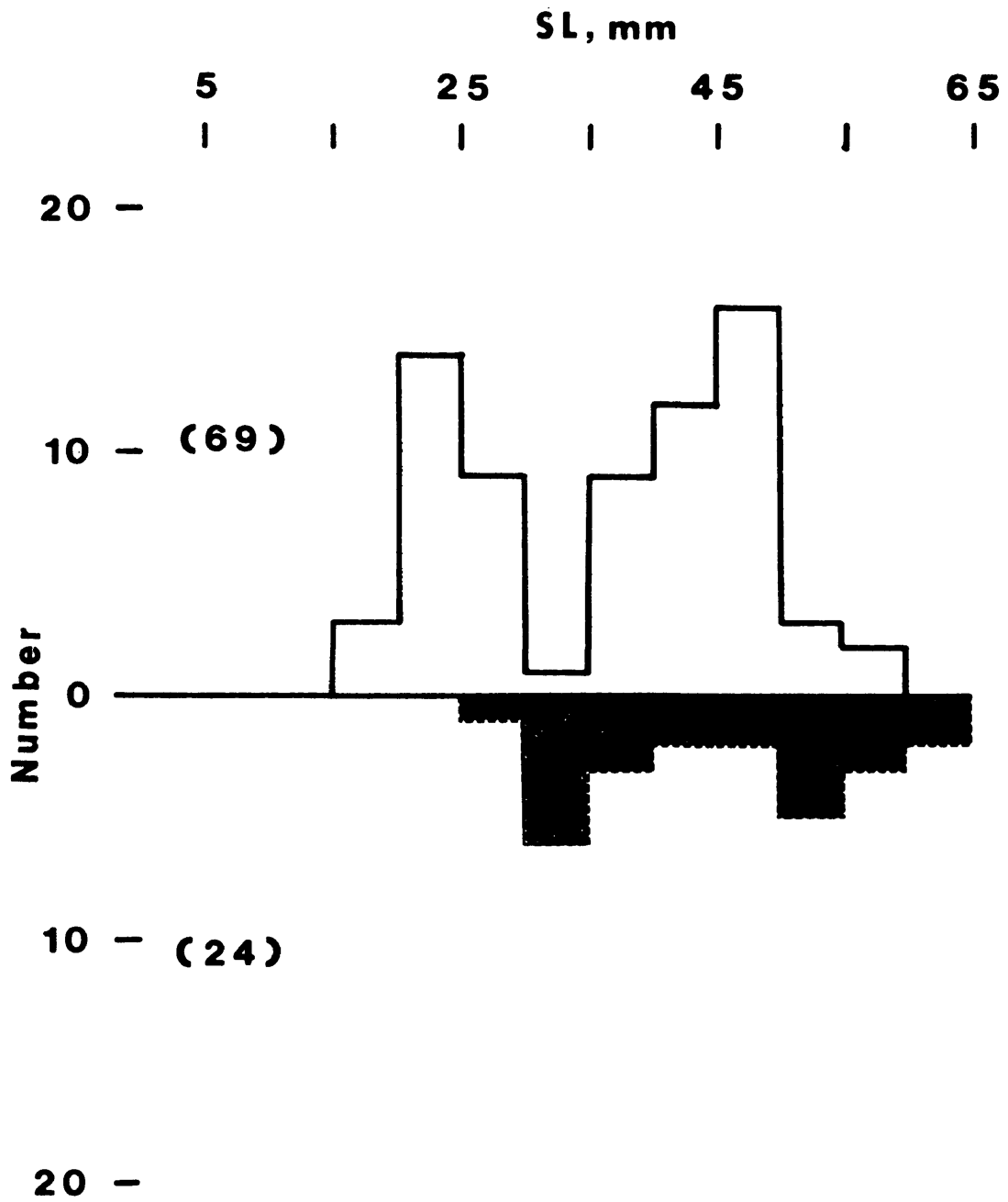


Fig. 4. Length frequencies for Cottus bairdi and Cottus girardi at Station 4 on August 27 and 28, 1977. Open bars indicate C. bairdi and shaded bars indicate C. girardi. Numbers in parentheses are sample sizes.



relatively higher). This trend becomes even more pronounced if we consider those fishes which were caught on the same day and at the same station (Table 4) (only May, June, and July are considered in this comparison since these are the months in which the young-of-the-year size range did not overlap with that for older fish). The SL range for C. girardi was always higher than that for C. bairdi. The SL of only one out of 14 C. girardi was within the range for C. bairdi from the same station and date. Sample sizes allow further testing of these interspecific differences at Station 4 on June 25, 1977 and July 25, 1976. Since the variances for SL data did not differ significantly between species on either date ($F_{4,4} = 1.145$, $p > 0.10$ and $F_{3,4} = 1.654$, $p > 0.10$), Student's t-tests were performed to determine if differences in mean SL between species were significant. In both cases C. girardi was significantly larger than C. bairdi ($t_8 = -5.006$, 2-tail $p < 0.01$ and $t_7 = 4.118$, 2-tail $p < 0.01$). It is also of interest that young C. bairdi were significantly smaller on June 24, 1977 at Station 5 than they were at Station 4 on the same date ($F_{4,5} = 5.798$, $p > 0.05$ and $t_9 = 5.436$, 2-tail $p < 0.01$).

Differences were also evident in egg development between these two species (Fig. 5). Female C. bairdi began to mature in the 30 to 40 mm size class, but C. girardi did not do so until 40 to 50 mm. A closer look at this data reveals that the smallest female C. girardi with definitely maturing ova (≥ 0.3 mm in diameter) were two fish of 45 mm SL that were found in August. The smallest female C. bairdi that contained maturing ova was a 34 mm SL fish found in November. Furthermore, in February and March all but one of the 17 female C. bairdi in the 35.5 to 45.0 mm

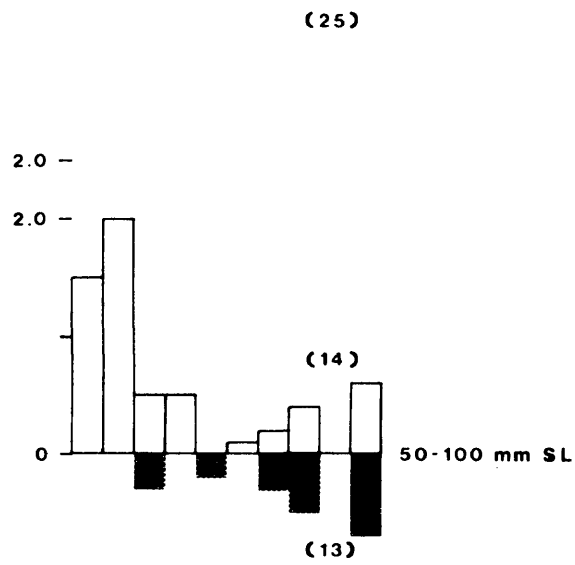
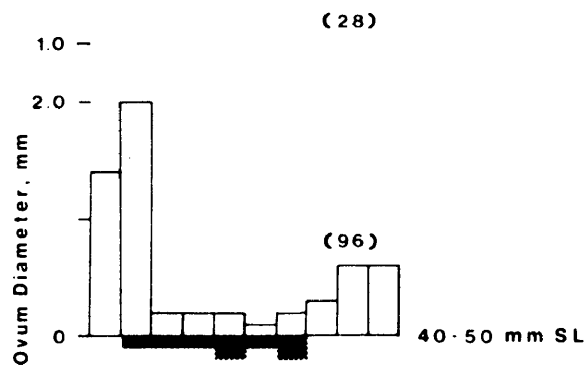
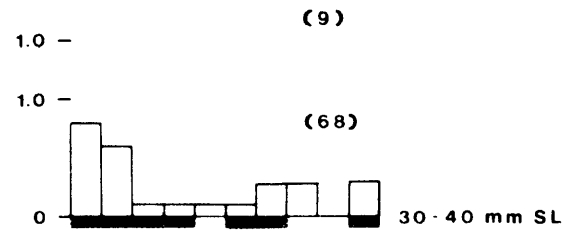
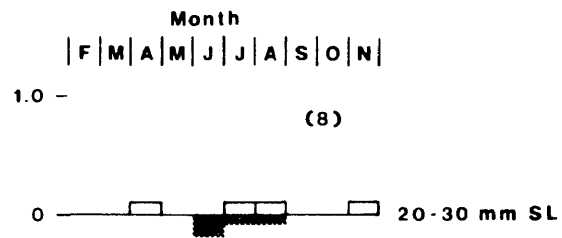
TABLE 4

SIZE RANGES FOR YOUNG-OF-THE-YEAR COTTUS BAIRDI AND COTTUS GIRARDI

Date	Station	Size Range (mm)	
		<u>C. bairdi</u>	<u>C. girardi</u>
5-11-77	4	6.5-9.0 (6)*	11.5 (2)
6-25-77	4	17.0-22.0 (5)	24.5-29.5 (5)
6-25-77	5	14.0-16.5 (6)	20.0-22.0 (2)
7-25-76	4	23.0-27.5 (5)	28.5-34.0 (4)
7-25-76	5	23.0-27.5 (3)	26.5 (1)

* Numbers in parentheses are sample sizes.

Fig. 5. Mean diameter of largest ova (oocytes) by month for female Cottus bairdi and Cottus girardi. All stations and dates combined for each month. Open bars indicate C. bairdi and shaded bars indicate C. girardi. Numbers in parentheses are sample sizes.



2.0 -

SL class contained large developing ova (> 1.0 mm in diameter), while none of the seven female C. girardi in this length class contained ova larger than 0.1 mm in diameter. It is also interesting in this regard to note that February and March are the only months in which no male or female C. girardi greater than 45.0 mm SL were taken (Figs. 2 and 3). Finally, there was a consistent pattern of C. girardi ova being larger than C. bairdi ova in September and November. This trend is based on only one C. girardi in each of these months, but in each case the range of values for C. bairdi females (seven specimens in September and ten specimens in November) does not overlap with the value for the single C. girardi female.

Only C. bairdi males were found with egg clusters. A total of 11 groups of eggs were found on the underside of flat rocks in moderate current (all at Station 4). Two of these were found on March 19, 1977 and nine were found on April 16, 1977. Male C. bairdi were closely associated with six clusters. Only one definitely mature C. girardi (an 81 mm female) was found in this area during this time period, and she was not associated with eggs. The young of both species, however, were found at Station 4 in May of 1977.

Hann (1927), Bailey (1952), and Ludwig and Lange (1975) all agree that C. bairdi matures at two years of age. Naked Creek C. bairdi seemed to range up to 35 or 40 mm (SL) near the end of their first year (in March and April). Thus, a two-year-old fish must be at least larger than 35 mm. Female C. bairdi began to mature between 30 and 40 mm while C. girardi matured at 40 to 50 mm. Also, male C. bairdi seemed

to be larger at a given age than did females [Bailey (1952) confirms this tendency]. Therefore, the SL of 45 mm was chosen to separate mature from immature fish of both species. All female C. bairdi and most female C. girardi should be mature at this size. The situation in males is less obvious, but the immature class should be free of mature males of either species.

FOOD HABITS

Introduction

There are many possible sources of variability in ecological field data. In addition to the variability associated with actual differences in resource use between species, we might expect variability due to sex, size, date, location, time of day, and, undoubtedly, many other factors. These sources of variability should be especially important in terms of food habits due to the seasonal occurrence, local abundance (or the lack of it), seasonal size differences, and diel activity patterns of benthic invertebrates. Ideally, therefore, food habits comparisons would be restricted to fish caught at the same station, on the same date, and at the same time. Unfortunately, the large amount of time spent measuring and recording habitat data usually restricted the sample size from any one station, date, and time. Most comparisons are thus between similar sized fish in a given season with all stations combined. At times it was also necessary to combine different sizes and/or sexes within a species in order to obtain useable sample sizes (ca. 10 fish).

This section includes the following: a summary of the overall food habits of each species, a comparison of monthly food habits using a purely numerical measure (mean number per stomach), a comparison of seasonal food habits using numerical, frequency of occurrence, dominance,

and overlap measures, and, finally, a summary of important trends in the preceding data.

Overall Food Habits for Each Species

The overall food habits of 327 C. bairdi and 142 C. girardi (Table 5) were quite similar. Only 2% of the total number of food items were from categories that were used by only one species (species-level identification of food items may or may not have altered this figure). Insecta (almost exclusively aquatic larvae) was the most important taxon in the diet of both species, and dipterans, ephemeropterans, and trichopterans were the most important insects.

Nevertheless, a few interspecific dietary differences are notable. Among the less important food items, nematodes (probably parasitic forms), gastropods, brachycerans, and baetids were more important in the diet of C. bairdi, and plant debris, oligochaetes, and copepods were more important to C. girardi.

Dipterans were more important food items for C. bairdi than for C. girardi. The most important group within this order, chironomids, occurred at about the same frequency in both species but was less important to C. girardi in terms of both numbers and dominance. Unidentified nematocerans were more important to C. girardi, but, even if all of these insects are assumed to be chironomids, the number and dominance values for the latter group are still much lower in C. girardi than in C. bairdi.

The reverse of this trend was found in the relative importance of ephemeropterans. Only two minor groups, Baetidae and Heptageniidae,

TABLE 5

OVERALL DIET OF COTTUS BAIRDI (b) AND COTTUS GIRARDI (g)

Food Item	% Frequency of Occurrence		% of Total Number		% Frequency of Occurrence as Dominant Item	
	b	g	b	g	b	g
Rocks	20	27	--	--	--	--
Vascular Plant						
Debris	8	13			<1	4
Filamentous						
Algae	29	34	--	--	1	1
<u>Hydra</u> sp.	<1	0	<1	0	0	0
Planariidae	<1	0	<1	0	<1	0
Nematoda	10	1	1	1	<1	0
Unidentified						
Gastropoda	6	1	1	<1	3	1
<u>Lioplax</u> sp.	1	0	<1	0	0	0
<u>Physa</u> sp.	1	0	<1	0	<1	0
Planorbidae	2	0	<1	0	<1	0
Total						
Gastropoda	--	--	1	<1	4	1
Oligochaeta	1	4	<1	2	0	3
Acari	4	2	<1	<1	1	0
Cladocera	2	1	<1	1	0	0
Ostracoda	<1	1	<1	<1	0	0
Amphipoda	0	1	0	<1	0	0
Copepoda	7	16	1	5	1	4
Cambarinae	1	0	<1	0	<1	0
Total						
Crustacea			2	6	1	4
Total Non-						
Insecta	--		5	9	9	15

TABLE % (Continued)

Food Item	% Frequency of Occurrence		% of Total Number		% Frequency of Occurrence as Dominant Item	
	b	g	b	g	b	g
Unidentified						
Insecta	17	19	1	2	0	0*
Unidentified						
Coleoptera	1	0	<1	0	<1	0
Hydroporinae	<1	1	<1	<1	0	0
Haliplidae	<1	0	<1	0	0	0
Gyrinidae	2	1	<1	<1	1	0
Chrysomelidae	<1	0	<1	0	0	0
Hydrophilidae	1	0	<1	0	0	0
Dryopidae	<1	0	<1	0	<1	0
<hr/>						
Total						
Coleoptera	--		<1	<1	2	0
<hr/>						
Unidentified						
Diptera	9	11	2	2	<1	
Unidentified						
Nematocera	12	20	4	7	<1	1
Simulidae	4	3	<1	1	<1	0
Chironomidae	65	64	67	36	30	18
Tipulidae	8	7	1	1	1	3
Heleinae	0	1	0	<1	0	1
Unidentified						
Brachycera	9	3	1	<1	1	0
Dolichopodidae	1	0	<1	0	<1	0
Empididae	5	2	1	<1	2	0
Muscidae	0	1	0	<1	0	1
<hr/>						
Total Diptera	--	--	76	49	35	24
<hr/>						
Unidentified						
Ephemeroptera	24	35	2	8	3	7
Baetidae	6	1	<1	<1	2	0
Caenis sp.	<1	1	<1	<1	0	<1
Ephemerella						
sp.	26	32	7	17	18	26
Heptageniidae	8	6	1	1	3	1
Paraleptophlebia						
sp.	0	1	0	<1	0	1

TABLE 5 (Continued)

Food Item	% Frequency of Occurrence		% of Total Number		% Frequency of Occurrence as Dominant Item	
	b	g	b	g	b	g
<u>Potamanthus</u>						
sp.	0	1	0	<1	0	0
Siphonuridae	8	8	1	1	3	5
<u>Tricorythodes</u>						
sp.	6	12	1	3	5	8
<hr/>						
Total						
Ephemeroptera	--	--	12	31	34	49
<hr/>						
<u>Sialis</u> sp.	1	3	<1	<1	1	2
Unidentified						
Anisoptera	0	1	0	<1	0	1
Gomphidae	1	1	<1	<1	1	1
Coenagrionidae	<1	1	<1	<1	0	0
<hr/>						
Total Odonata	--	--	<1	<1	1	1
<hr/>						
Unidentified						
Plecoptera	4	2	<1	<1	1	0
<u>Allocapnia</u> sp.	1	1	<1	<1	<1	0
<u>Pteronarcys</u> sp.	1	0	<1	0	<1	0
Perlidae	2	3	1	1	1	3
<hr/>						
Total						
Plecoptera	--	--	1	1	2	3
<hr/>						
Unidentified						
Trichoptera	10	6	1	1	4	1
<u>Glossosoma</u> sp.	1	0	<1	0	<1	0
Hydropsychi-						
dae	19	5	2	1	8	3
Hydroptilidae	11	13	2	5	4	4
Leptoceridae	1	0	<1	0	1	0
Lepidostoma-						
tidae	<1	0	<1	0	0	0
<u>Psilotreta</u> sp.	<1	0	<1	0	0	0
Polycentropus						
sp.	<1	2	<1	<1	0	0
<hr/>						
Total						
Trichoptera	--	--	5	7	16	8

TABLE 5 (Continued)

Food Item	% Frequency of Occurrence		% of Total Number		% Frequency of Occurrence as Dominant Item	
	b	g	b	g	b	g
<u>Total Insecta</u>	--	--	96	91	92	86
Unidentified						
Pisces	3	2	<1	<1	1	0
<u>Etheostoma</u>						
<u>flabellare</u>	0	2	0	<1	0	2

*Fish containing only unidentifiable insect remains were not included in dominance calculations.

were more important to C. bairdi, while unidentified ephemeropterans, ephemereids, and tricorythids were all more important (by all three measures) to C. girardi.

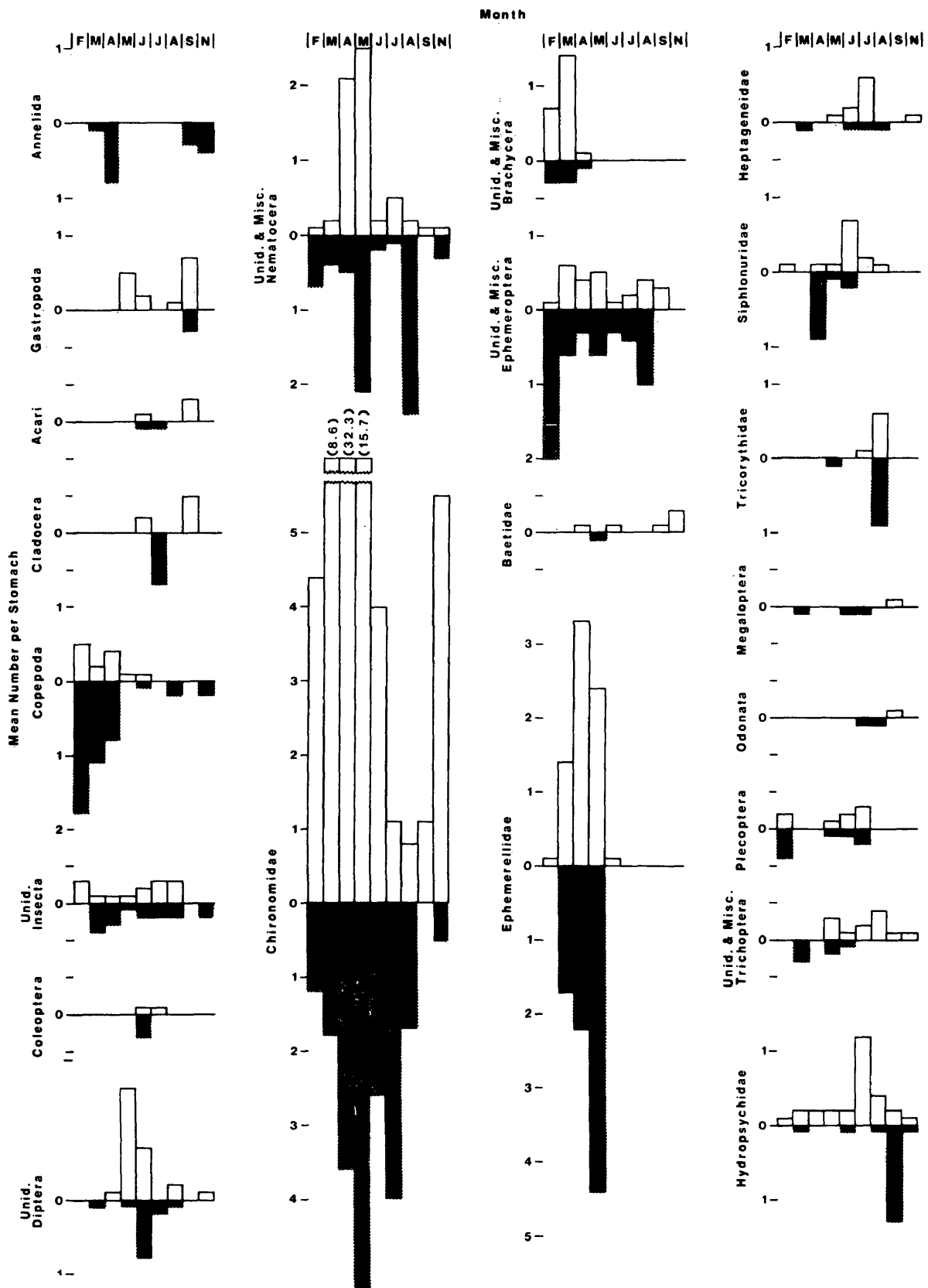
Trichopterans were more important by number in C. girardi stomachs and by dominance in C. bairdi stomachs. This could be due to the fact that Hydroptilidae was the most important family for C. girardi, and Hydropsychidae was the most important family for C. bairdi. Hydroptilids are generally much smaller than hydropsychids and are thus less likely to be the dominant volumetric component of an individual stomach even if they are eaten in relatively large numbers.

Monthly Comparisons

Data on the mean numbers per stomach for most of the important food categories (Fig. 6) illustrate and clarify several of the trends that were noted in the previous section. Some groups that were of minor importance in the overall data were seasonally important, and some of the trends noted in major food groups were not consistent from month to month or from station to station.

In the preceding section nematodes, gastropods, baetids, brachycerans, hydropsychids, and chironomids were found to be more important in the diet of C. bairdi than in that of C. girardi. Too few nematodes were eaten for them to appear in Fig. 6. Gastropods were not very important food items, but, when they were eaten, they were always eaten in larger numbers by C. bairdi. The significance of the difference in the one month during which C. girardi also ate moderate numbers of snails

Fig. 6. Mean number per stomach per month for several major food items in Cottus bairdi and Cottus girardi. Open bars indicate C. bairdi and shaded bars indicate C. girardi. Sample sizes for C. bairdi and C. girardi respectively are 36 and 6 (February), 41 and 19 (March), 56 and 13 (April), 32 and 29 (May), 38 and 19 (June), 26 and 13 (July), 62 and 30 (August), 15 and 3 (September), and 21 and 11 (November).



(September) was not evaluated statistically due to the large number of zero-zero ties between species (these tend to make the tests too conservative). Baetids were never eaten in large numbers and never by both species in the same month. C. bairdi did, however, eat them more often throughout the year (these were Pseudocloeon). Brachycerans definitely seem to have been more important to C. bairdi in February and March, but this difference could only be tested on March 19, 1977. On this date immatures of both species ate significantly fewer brachycerans than did male C. bairdi ($p < 0.02$ for immature C. bairdi and < 0.002 for immature C. girardi). The difference noted in the use of hydropsychids was that C. bairdi ate them more consistently throughout the year. There were, however, large differences in July when C. bairdi ate larger numbers and in September when C. girardi ate larger numbers.

The numbers of chironomids eaten by both species exhibited marked and complex fluctuations. In every month except July and August, the mean number per stomach for C. bairdi was higher than that of C. girardi. Significant interspecific differences were, however, found only in March, April, and August (Table 6). On March 5, 1977 the group eating the largest number of chironomid larvae (and the group primarily responsible for the large difference seen in Fig. 6) was immature C. bairdi from Station 1. These fish ate significantly more chironomids than did any other group. Adult C. bairdi ate the next largest number followed by immature C. bairdi at Station 3 and immature C. girardi. Therefore, immature C. girardi from Station 2 ate significantly less chironomids than did immature C. bairdi from just downstream at Station 1 or adult C. bairdi

TABLE 6

MANN-WHITNEY (two groups) OR KRUSKAL-WALLIS (more than two groups)
 TESTS OF THE SIGNIFICANCE OF DIFFERENCES IN NUMBERS OF
 CHIRONOMID LARVAE EATEN BY COTTUS BAIRDI (b) AND COTTUS GIRARDI
 (g). (H_0 : two or more samples are drawn from populations having the
 same parent distribution) (m = male, f = female, a = adult, and i =
 immature).

Date	Stations Tested	Groups Tested*	Two-tail p
2-10-77	3, 4, 5	mb, fb, ib, ig	> 0.10
3-5-77	1, 3	ib	< 0.05
3-5-77	1, 2, 3, 5	mb, fb, ib (Station 1), ig	< 0.01
3-5-77	1, 3, 5	ab, ib (Station 1)	=0.05
3-5-77	1, 3, 5	fb, ib (Station 1)	=0.016
3-5-77	2, 3, 5	fb, ig	=0.072
3-5-77	2, 3, 5	ab, ig	=0.002
3-5-77	1, 2	ib (Station 1), ig	=0.016
3-5-77	3, 5	mb, fb, ib (Station 3)	> 0.30
3-5-77	2, 3	ib (Station 3), ig	> 0.11
3-19-77	3, 4	mb, ib, ig	> 0.50
4-16-77	4, 5	ib	< 0.002
4-16-77	4, 5	ig	=0.832
4-16-77	4, 5	mb, fb, ib (Station 4), ig	< 0.001
4-16-77	4, 5	mb, fb, ib (Station 4)	> 0.10
4-16-77	4, 5	all b (Station 4), ig	< 0.00006
4-16-77	4, 5	mb, fb, ib (Station 5), ig	< 0.02
4-16-77	4, 5	mb, fb, ib (Station 5)	> 0.10
4-16-77	4, 5	all b (i at Station 5), ig	< 0.02

TABLE 6 (Continued)

Date	Stations Tested	Groups Tested*	Two-tail p
5-11-77	1, 4	ib	< 0.001
5-11-77	1, 2, 4	ig	< 0.01
5-11-77	1	ib, mg, fg, ig	> 0.10
5-11-77	4	mb, fb, ib, mg, ig	> 0.20
6-20-76	5	mb, ib, fg, ig	> 0.50
6-25-77	4, 5	ib	> 0.10
6-25-77	4, 5	ab, ib, ag, ig	> 0.10
7-25-76	4, 5	ib	> 0.858
7-25-76	4, 5	ab, ib, ig	> 0.50
8-27, 28-77	4	ib (between dates)	> 0.10
8-27, 28-77	4	ig (between dates)	= 0.008
8-27-77	4	ab, ib, ag, ig	> 0.50
8-28-77	4	ib, ig	= 0.002
11-1-76	4, 5	all b, all g	> 0.10

*See Appendix B for sample sizes used in these tests.

from upstream at Stations 3 and 5 (the latter difference must have been primarily due to male C. bairdi since the difference between female C. bairdi and immature C. girardi was not significant). Immature C. bairdi at Station 3 were intermediate between adult C. bairdi and immature C. girardi. No significant difference was detected among male C. bairdi, immature C. bairdi, and immature C. girardi on March 19, 1977. In April all comparisons indicated that C. bairdi ate significantly more chironomids. The one significant difference detected in August, however, was in the opposite direction. A significant diel difference is indicated for immature C. girardi by this data. Those caught on the afternoon (1355 to 1855 hours) of August 27, 1977 ate significantly fewer chironomid larvae than did those from the morning (0630 to 0755 hours) of August 28, 1977. The latter group also ate significantly larger numbers than did immature C. bairdi caught during the same time period.

Vascular plant debris, oligochaetes, hydroptilids, copepods, and ephemeropterans (especially ephemereids and tricorythids) were mentioned in the preceding section as being more important to C. girardi than to C. bairdi. Vascular plant debris does not appear in Fig. 6 since it is difficult to assign a number to pieces of plant material. The numbers of oligochaetes eaten by C. bairdi were never large enough to appear in this figure, but those eaten by C. girardi were this large in March, April, September, and November. Hydroptilid numbers were never very large for either species in any given month.

Copepods were mainly winter and spring food items for both species but were generally eaten in larger numbers by C. girardi. These numbers

were, however, only large enough on one date to allow statistical testing (Table 7). On this date (March 19, 1977) immature C. girardi ate significantly greater numbers of copepods than did either male or immature C. bairdi. In fact, 1 out of 24 C. bairdi had eaten copepods, while 7 out of 11 C. girardi had eaten them.

Data for the various groups of ephemeropterans are similar in complexity to those for chironomids. Significant interspecific differences were found in February, March, and April (Table 8). In February immature C. girardi ate significantly more ephemeropterans than did male, female, or immature C. bairdi. On March 5, 1977 there were no significant interspecific differences in the numbers of ephemerellids eaten, but immature C. bairdi did eat significantly larger numbers at Station 3 than at Station 1. On March 19, 1977 immature C. bairdi from Station 3 ate significantly more ephemerellids than did male C. bairdi from Station 4 but not more than did immature C. girardi from Stations 3 and 4. It is also interesting to note that, contrary to data for March 5, immature C. bairdi ate more ephemerellids at a more downstream station (Station 3) than they did at a more upstream station (Station 4). Results for April 16, 1977 are complicated, but immature C. bairdi did eat significantly more ephemerellids at Station 4 than did immature C. girardi. Neither species ate many of these insects at Station 5. Also, on August 27 and 28, 1977 a diel pattern was evident for immature C. bairdi with more ephemeropterans being eaten in the morning of the 28th than in the evening of the 27th. Numbers of tricorythids were never large enough to test statistically, but the difference noted in the preceding section is evident (although not large) in Fig. 6.

TABLE 7

MANN-WHITNEY OR KRUSKAL-WALLIS TESTS OF THE SIGNIFICANCE OF DIFFERENCES IN NUMBERS OF COPEPODS EATEN BY COTTUS BAIRDI AND COTTUS GIRARDI. (See Table 6 for further explanation).

Date	Stations Tested	Groups Tested	Two-tail p
3-19-77	3, 4	ib	> 0.10
3-19-77	3, 4	ig	> 0.922
3-19-77	3, 4	mb, ib, ig	< 0.001
3-19-77	3, 4	mb, ib	> 0.10
3-19-77	3, 4	allb, ig	< 0.00014

TABLE 8

MANN-WHITNEY OR KRUSKAL-WALLIS TESTS OF THE SIGNIFICANCE OF DIFFERENCES IN NUMBERS OF EPHEMEROPTERAN LARVAE EATEN BY COTTUS BAIRDI AND COTTUS GIRARDI. (See Table 6 for further explanation).

Date	Food Category	Stations Tested	Groups Tested	Two-tail p
2-10-77	Total			
	Ephemeropterans	3, 4, 5	mb	> 0.10
2-10-77	"	3, 4, 5	ib	> 0.200
2-10-77	"	3, 4, 5	mb, fb, ib, ig	< 0.05
2-10-77	"	3, 4, 5	mb, fb, ib	> 0.50
2-10-77	"	3, 4, 5	allb, ig	=0.0032
3-5-77	Ephemerellids	1, 3	ib	< 0.021
3-5-77	"	1, 2, 3, 5	mb, fb, ib (Station 1), ig	> 0.30
3-5-77		1, 2, 3, 5	mb, fb, ib (Station 3), ig	> 0.10
3-19-77	"	3, 4	ib	=0.05
3-19-77	"	3, 4	ig	=0.376
3-19-77	"	3, 4	mb, ib (Station 3), ig	< 0.05
3-19-77		3, 4	mb, ib (Station 4), ig	> 0.10
3-19-77	"	3, 4	mb, ib (Station 3)	< 0.02
3-19-77	"	3, 4	mb, ig	> 0.10
3-19-77	"	3, 4	ib, ig	> 0.10
4-16-77	"	4, 5	ib	< 0.002
4-16-77	"	4, 5	ig	≈ 1.00
4-16-77	"	4, 5	mb, fb, ib (Station 4), ig	< 0.01
4-16-77		4, 5	mb, fb, ib (Station 4)	> 0.50

TABLE 8 (Continued)

Date	Food Category	Stations Tested	Groups Tested	Two-tail p
4-16-77	EphemereUids	4, 5	all b (i at Station 4) ig	<0.0007
4-16-77	"	4	ib, ig	=0.002
5-11-77	"	1, 4	ib	>0.280
5-11-77	"	1, 2, 4	ig	>0.70
5-11-77	"	1, 2, 4	mg, fb, ib, mg, fg, ig	>0.50
7-25-76	Total			
	Ephemeropterans	4, 5	ib	=0.858
7-25-76	"	4, 5	ab, ib, ig	>0.30
8-27, 28-77	"	4	ib (between dates)	<0.002
8-27, 28-77	"	4	ig (between dates)	=0.15
8-27-77	"	4	ab, ib, ag, ig	>0.50
8-28-77	"	4	ib, ig	>0.10

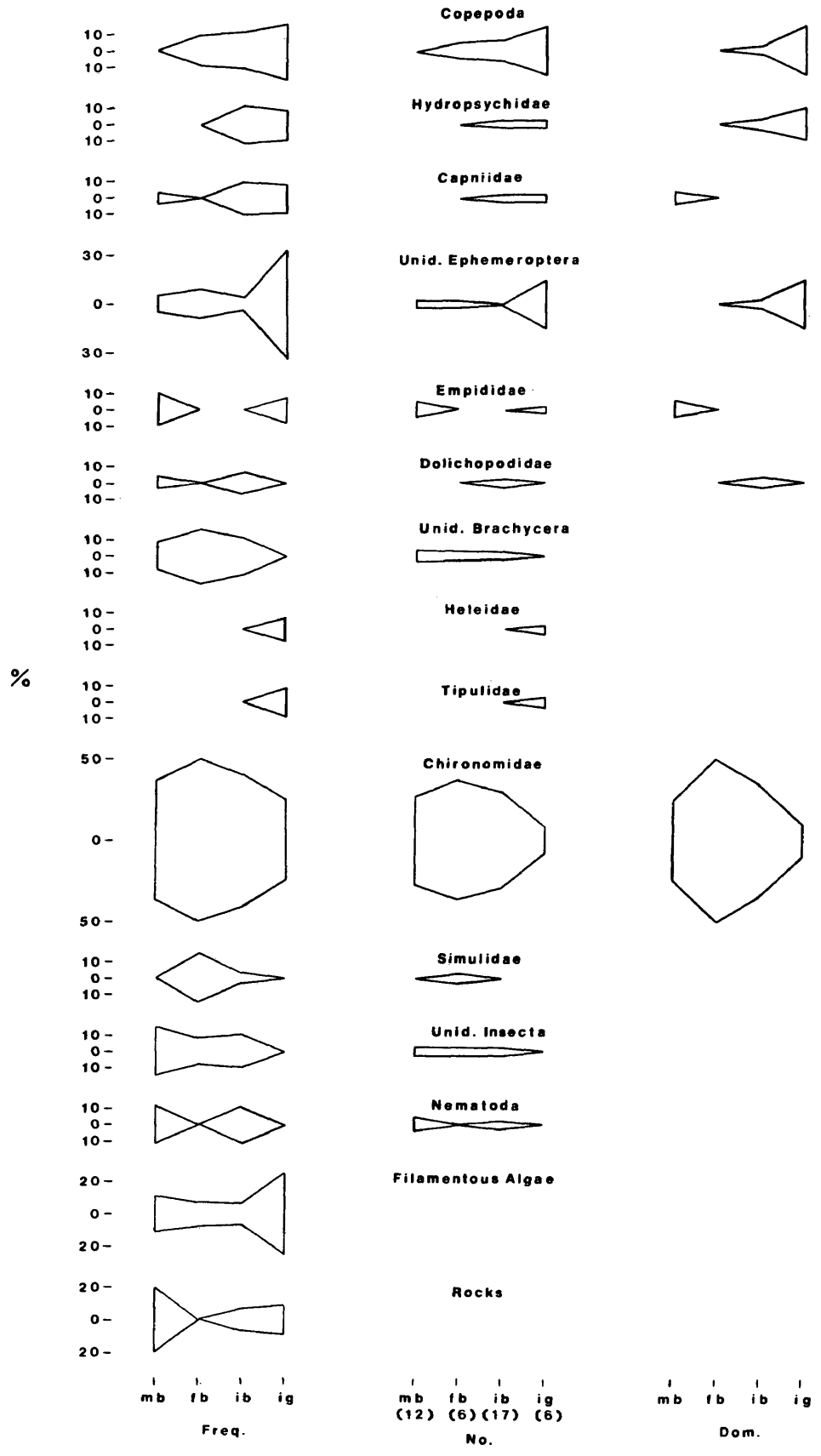
Among those items not indicated as being of interest in the previous section, cladocerans, heptageneids, and siphonurids were of seasonal importance. Cladocerans were never eaten by both species of sculpin in a given month, but were eaten in similar numbers by immatures of both species plus female C. bairdi. Heptageneid mayflies attained a level of importance in C. bairdi in July that they never approached in C. girardi. Both species, however, had definite peaks in their usage of siphonurid mayflies. These were of roughly the same magnitude but were in different months.

Seasonal Comparisons

Winter: Dipterans formed an important part of the diet of both species in winter (Fig. 7). In all three groups of C. bairdi, chironomids were the most important group (by all three of the methods used). Only immature C. girardi were collected in winter, but these exhibited quite a different diet from that of any of the C. bairdi groups. Chironomids ranked third in percent dominance and percent total number in these fish. Also the values for chironomids by any of the three methods were much less for immature C. girardi than for any group of C. bairdi. Of the miscellaneous groups in this order, unidentified Brachycera, Dolichopodidae, and Simuliidae were eaten only by C. bairdi, while Tipulidae and Heleidae were eaten only by C. girardi. Empidids were eaten only by male C. bairdi and immature C. girardi.

The situation regarding Ephemeroptera was the opposite of that seen in Chironomidae. By all three of the measures used, unidentified

Fig. 7. Major winter foods of Cottus bairdi and Cottus girardi as percent frequency of occurrence (Freq.), percent total number (No.) and percent frequency of occurrence as dominant item (Dom.). Abbreviations for species and size groups as before. Numbers in parentheses at bottom of figure are sample sizes.



mb fb ib ig
Freq.

mb fb ib ig
(12) (6) (17) (6)
No.

mb fb ib ig
Dom.

ephemeropterans (most of these were tiny early instar larvae) were much more important to C. girardi than to C. bairdi. This group also seemed to be the most important group overall for C. girardi.

Copepods offer another possible dietary difference between these species. C. girardi ate more of these crustaceans than did any group of C. bairdi. This difference was especially marked in terms of dominance and numbers. It is noteworthy that male C. bairdi ate no copepods, while females and immatures made use of them fairly often.

Among the less important groups rocks, filamentous algae, nematodes, and hydropsychids are of interest. Rocks were most common in the stomachs of male C. bairdi, filamentous algae occurred twice as often in C. girardi as it did in any group of C. bairdi, and nematodes occurred only in male and immature C. bairdi. Hydropsychids, relatively large food items, occurred only in the two immature groups and were more common in immature C. bairdi but more important by the dominance method in immature C. girardi. A further analysis of this data indicates that immature C. bairdi consumed members of the genera Cheumatopsyche and Hydropsyche plus unidentified hydropsychids, while immature C. girardi consumed only one Cheumatopsyche. The similar percentages in Fig. 7 are, of course, due to the relatively smaller sample size for immature C. girardi.

Overlap values within C. bairdi were much higher than those between C. bairdi and C. girardi (Table 9). If we use the rule-of-thumb that overlap values greater than 0.60 are significant, then all pairwise comparisons within C. bairdi indicate significant overlap, and no comparisons

TABLE 9

WINTER DIET OVERLAP (D) BETWEEN COTTUS BAIRDI AND COTTUS GIRARDI. ABBREVIATIONS FOR SPECIES AND SIZE GROUPS AS IN TABLE 6.

	mb	fb	ib
mb	--		--
fb	.66	--	
ib	.76	.77	--
ig	.36	.39	.47

between C. bairdi and C. girardi indicate significant overlap. The highest overlap values are between both groups of mature C. bairdi and immature C. bairdi, while the lowest values are between both groups of mature C. bairdi and immature C. girardi.

Spring: Dipterans were quite important in the diet of both species in spring (Fig. 8). Again, this fact was mainly due to the family Chironomidae, and, again, this family was more important (by number and dominance) to C. bairdi. Within C. bairdi males and immatures ate the most chironomids, and they were most often dominant in males. Unidentified nematocerans were much more common in adult C. girardi than in any other group, and some of these larvae may have been chironomids. Nevertheless, even if all of them were chironomids, there would be almost no difference in the frequency of occurrence of this family in adult C. girardi since almost all of the fish which contained unidentified nematocerans also contained chironomids. Also, the additional numbers contributed to Chironomidae by this unidentified group would not significantly effect the conclusions presented above. Brachycerans were used mostly by adult C. bairdi (especially males). Contrary to winter data, simuliids and tipulids were eaten by both species in spring, but they were still most important to female C. bairdi.

Among the ephemeropterans the most important family was Ephemeroptera. This family was more important to adult C. girardi (by all measures) than to any other group. Among the less important mayfly families, siphonurids were probably more important to immature C. girardi than to any other group but were totally absent in adult C. girardi.

Fig. 8. Major spring foods of Cottus bairdi and Cottus girardi as percent frequency of occurrence, percent total number, and percent frequency of occurrence as dominant item. Abbreviations for species and size groups as before. Numbers in parentheses at bottom of figure are sample sizes.

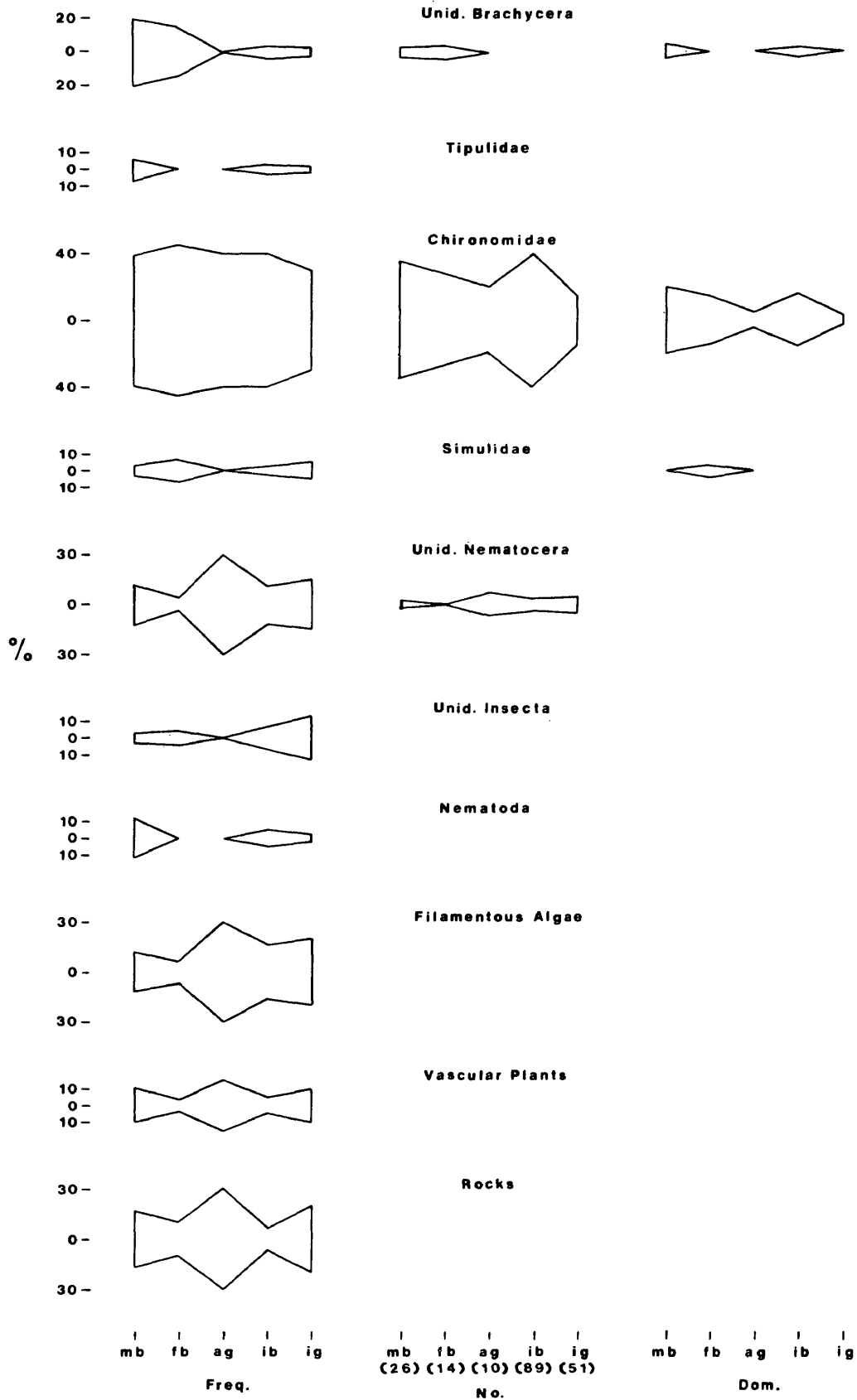
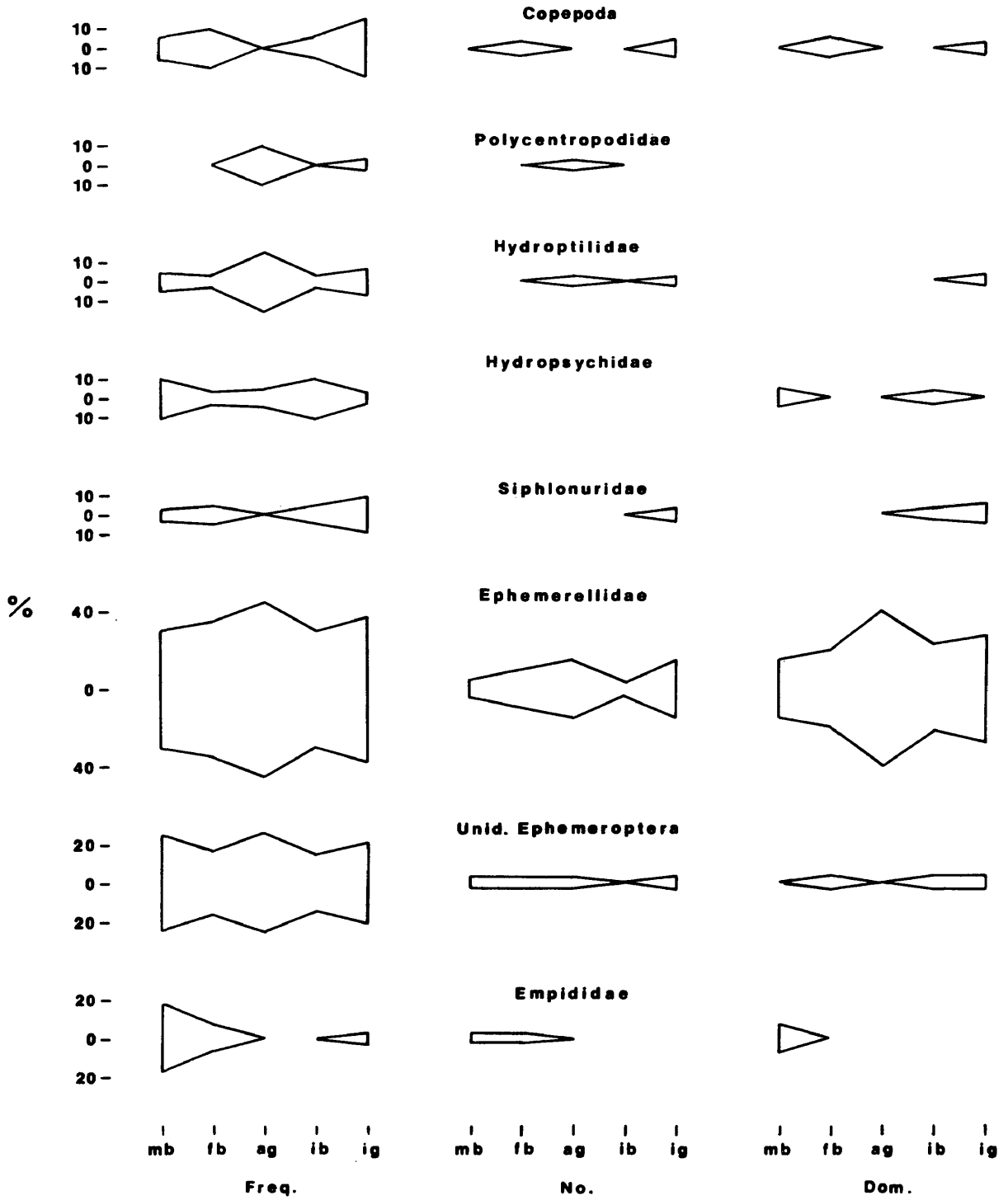


Fig. 8 (cont.)



The genus Isonychia occurred in female C. bairdi, immature C. bairdi, and immature C. girardi but was relatively more important in the latter group. One Ameletus was found in an immature C. girardi, and one Siphonurus was found in both an immature and a male C. bairdi. Most of the difference noted in Fig. 8, however, is due to the fact that unidentified siphonurids were relatively much more numerous in immature C. girardi than in any other group. Potamantids (not shown in Fig. 8) were only eaten by adult C. girardi, while Pseudocloeon (Baetidae) was eaten in small numbers by immatures of both species.

Trichopteran were also of some importance to both species in spring. Hydropsychidae was the most important family to male and immature C. bairdi. Hydropsychids that were not identifiable past the family level were eaten in small numbers by all three groups of C. bairdi but not by C. girardi. Members of the genus Cheumatopsyche were found in male and immature C. bairdi plus immature C. girardi but were relatively much more numerous in C. bairdi (especially males). Hydropsyche occurred in small numbers in the stomachs of male and immature C. bairdi plus female C. girardi. Hydroptilidae, the other important family in this order, was more important to both size classes of C. girardi. By far the most important genus in this family, Hydroptila, was eaten by all fish groups except female C. girardi and was relatively most numerous in male and immature C. girardi. A numerically unimportant genus, Oxyethira, occurred only in immature C. girardi. Finally, Polycentropodids were also only eaten by C. girardi.

Several less important groups are also of interest. Rocks, vascular

plant debris, and filamentous algae were all most common in adult C. girardi. Nematodes appeared in immature C. girardi but were most common in male and immature C. bairdi. Finally, copepods seem to have been most important in female C. bairdi and immature C. girardi.

Again, all intraspecific comparisons revealed significant dietary overlap (Table 10). In addition to these comparisons, however, overlap was also significant between all groups of C. bairdi and male C. girardi and between female C. bairdi and immature C. girardi. The pair with the highest overlap was male C. bairdi-immature C. bairdi, and the pairs with the lowest overlap were male C. bairdi-female C. girardi and immature C. bairdi-female C. girardi.

Summer: Once again the order Diptera was an important food group, although not to the extent that it was in spring (Fig. 9). The numerical importance of chironomids in immature C. bairdi decreased drastically from spring values, while that in immature C. girardi remained relatively constant. The summer dominance value for this group was less than the spring value in immature C. bairdi but four times greater than the spring value in immature C. girardi. All mature groups ate fewer chironomids in the summer. This family was more important (by both number and dominance) to female C. bairdi than to any other mature group. The only other important dipteran family, Tipulidae, was eaten most often by female C. girardi but was not eaten at all by male C. girardi. Again, simuliids were eaten only by C. bairdi (males and immatures).

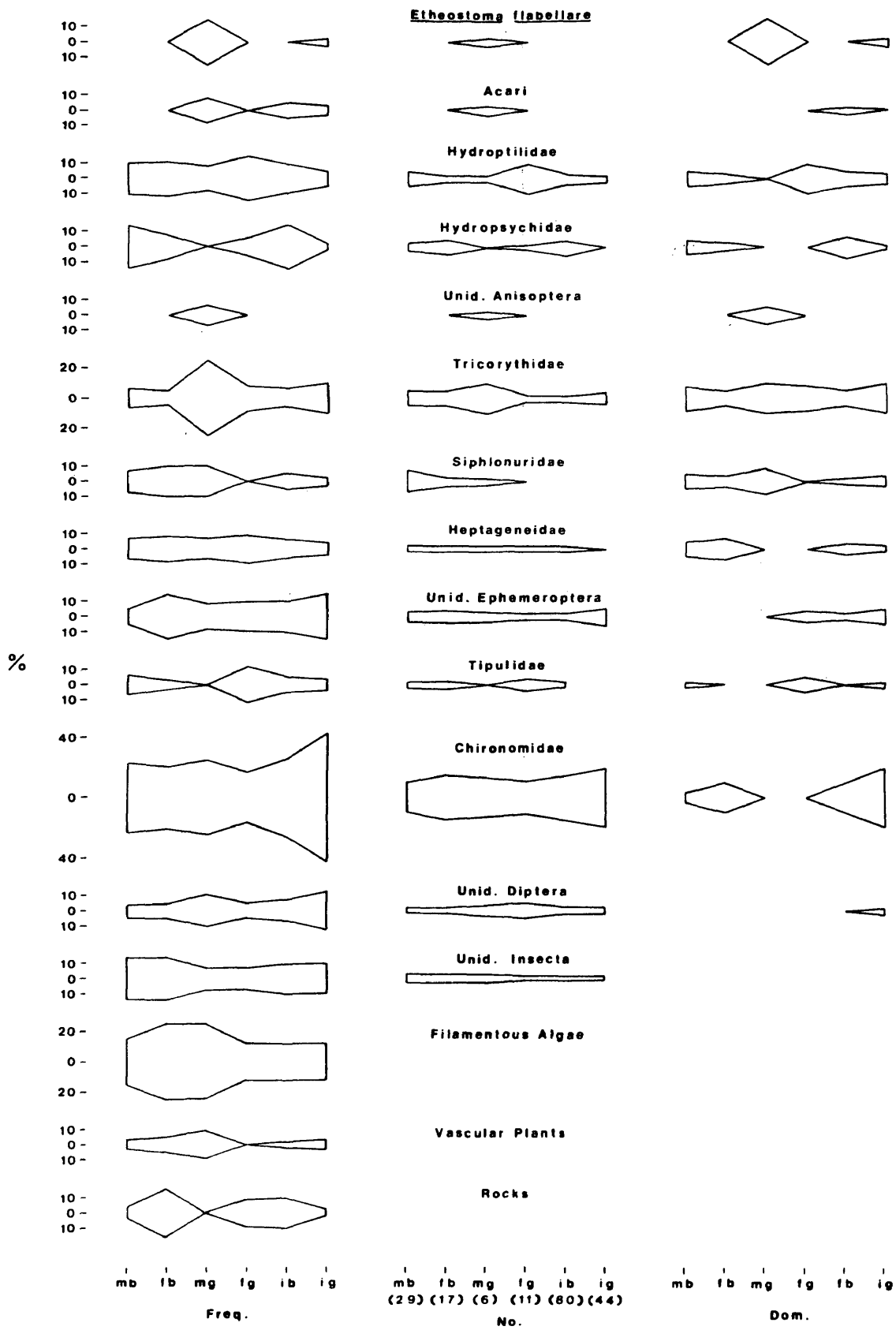
Ephemerellids were not important food items in summer, but three other families of mayflies, Tricorythidae, Siphonuridae, and Hepta-

TABLE 10

SPRING DIET OVERLAP (D) BETWEEN COTTUS BAIRDI AND COTTUS GIRARDI.
 ABBREVIATIONS FOR SPECIES AND SIZE GROUPS AS IN TABLE 6.

	mb	fb	ib	mg	fg
mb	--	--	--	--	--
fb	.77	--		--	
ib	.96	.77			
mg	.69	.79	.69	--	
fg	.36	.48	.36	.65	--
ig	.54	.69	.52	.72	.67

Fig. 9. Major summer foods of Cottus bairdi and Cottus girardi as percent frequency of occurrence, percent total number, and percent frequency of occurrence as dominant item. Abbreviations for species and size groups as before. Numbers in parentheses at bottom of figure are sample sizes.



geneidae, were of importance. Tricorythids were most common and most numerous in male C. girardi stomachs, but dominance values were similar in all sizes of both species of sculpin. Siphonurids were most important in adult C. bairdi and male C. girardi. Female C. girardi were the only fish that did not eat these mayflies. All siphonurids that were keyed to genus were Isonychia. This genus was of similar numerical importance in female C. bairdi, immature C. bairdi, and immature C. girardi. The difference noted in Fig. 9 is primarily due to siphonurids that were not identifiable beyond family. Heptageneids were somewhat more important in mature C. bairdi than in any of the other fish groups. Again, this difference is mainly due to those heptageneids that were not identifiable beyond family. Of the genera that were identified, Stenonema was eaten by male C. bairdi, immature C. bairdi, and female C. girardi; Epeorus was eaten only by immature C. bairdi; and Stenacron was eaten by female C. bairdi, immature C. bairdi, and male C. girardi. The relatively unimportant family Baetidae was eaten only by C. bairdi (all three groups).

Two families of caddisflies were important summer food items. Hydropsychids were most important in C. bairdi (especially males and immatures). The only fish that did not eat hydropsychids were male C. girardi. Cheumatopsyche was found in all three groups of C. bairdi plus immature C. girardi, but the relative numbers of this genus were much higher in C. bairdi (especially immatures). Hydropsyche was found only in C. bairdi and was relatively most numerous in females. Hydroptilids were eaten by all fish groups but were most important to female C. girardi.

The most important genus in this family, Hydroptila, was eaten in moderate numbers by male C. bairdi, immature C. bairdi, and female C. girardi and in lesser numbers by immature C. girardi. In addition, six Oxyethira were eaten in summer; all of these were eaten by immature C. girardi.

Four families of caddisflies which were not important enough to appear in Fig. 9, Leptoceridae, Polycentropodidae, Glossosomatidae, and Odontoceridae, were only eaten by C. bairdi.

Again, several less important groups are of interest. Gastropods and nematodes (which do not appear in Fig. 9) were eaten only by C. bairdi, while Etheostoma flabellare and dragonflies (Anisoptera) were only eaten by C. girardi. Rocks were most common in female C. bairdi, vascular plant debris in female C. bairdi and male C. girardi, and filamentous algae in adult C. bairdi and male C. girardi.

All dietary overlap values were relatively high in summer (Table 11). Contrary to data for the two previous seasons, however, two intraspecific pairs, male C. girardi-female C. girardi and immature C. girardi-female C. girardi did not quite overlap significantly in diet ($D = 0.58$ in both cases). All overlap values for this season are greater than 0.54 with the largest being between female and immature C. bairdi and the smallest being between female C. bairdi and female C. girardi.

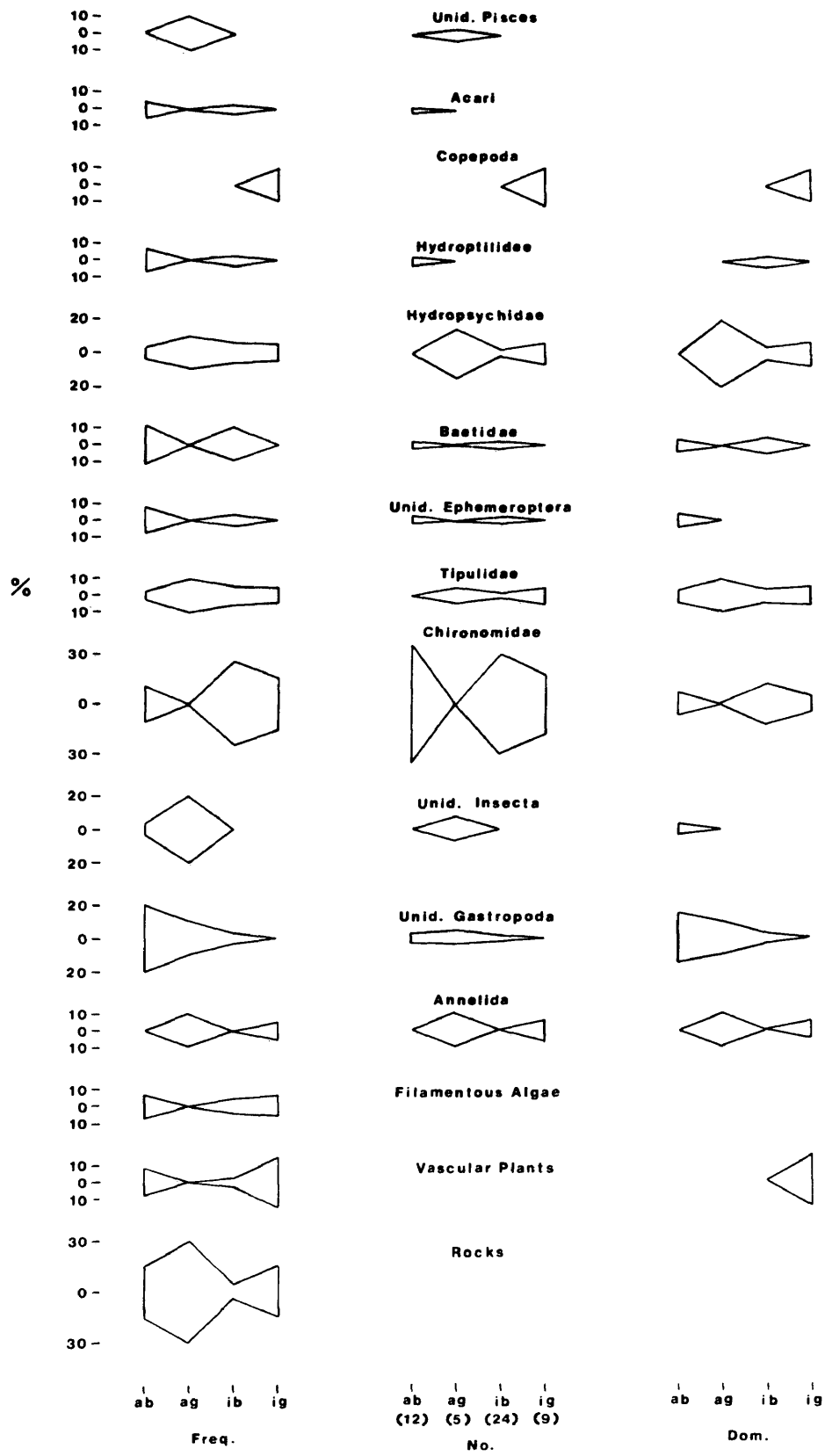
Fall: Only two families of dipterans were important fall food items (Fig. 10). The use of chironomids in fall was similar to that in spring. C. bairdi ate large numbers of these fly larvae relative to C. girardi. This trend seems to hold for all groups of both species but is most marked

TABLE 11

SUMMER DIET OVERLAP (D) BETWEEN COTTUS BAIRDI AND COTTUS GIRARDI. ABBREVIATIONS FOR SPECIES AND SIZE GROUPS AS IN TABLE 6.

	mb	fb	ib	mg	fg
mb	--	--	--	--	--
fb	.73	--			
ib	.71	.77	--	--	
mg	.62	.65	.62	--	
fg	.69	.54	.68	.58	--
ig	.62	.73	.68	.72	.58

Fig. 10. Major fall foods of Cottus bairdi and Cottus girardi as percent frequency of occurrence, percent total number, and percent frequency of occurrence as dominant item. Abbreviations for species and size groups as before. Numbers in parentheses at bottom of figure are sample sizes.



in adults since adult C. girardi ate no chironomids in fall. Tipulids, however, were somewhat more important (by all three measures) to adult C. girardi than to any other group. Again, simuliids were eaten only by female C. bairdi.

Among the ephemeropterans, only small, unidentified forms, baetids, and heptageneids (which do not appear in Fig. 10) were eaten in fall. All three of these groups were absent in C. girardi stomachs, whereas C. bairdi ate them frequently though not in large numbers.

Hydropsychids were the most important family of caddisflies eaten in fall. According to Fig. 10, this family was much more important to adult C. girardi than to any other group. A closer look at this data, however, reveals that this difference is not so clear cut. Only two hydropsychids were not keyed beyond family, and immature of both fish species contained one of these caddisflies. Cheumatopsyche was eaten in small numbers by both male and immature C. bairdi. Hydropsyche was eaten by both immature C. bairdi and female C. girardi but in relatively greater numbers by the latter group. On the other hand, only C. bairdi contained hydroptilids and two families not appearing in Fig. 10, Leptoceridae and Glossosomatidae.

Gastropods assumed a greater importance, especially in terms of dominance, in fall than in any other season. Mature C. bairdi made greater use of this food item than did any other group.

Annelids and copepods, however, were found only in C. girardi. Both of these groups were fairly important in terms of dominance and frequency of occurrence. Annelids were also significant in terms of numbers.

It is indicative of the small amount of food eaten by C. girardi in this season that a relatively small food item such as copepods (which were eaten in small numbers) was dominant by volume in two fish (12% of the total number of specimens).

Also interesting in this regard is the fact that two non-food or accidental food items, rocks and vascular plant debris, were very important in the gut contents of C. girardi in fall. Rocks occurred much more frequently than any other item in C. girardi, and vascular plant debris tied with chironomids for second place in this category. Vascular plant debris was also important to immature C. girardi in terms of dominance.

Among the less important groups, fish were eaten only by male C. girardi, and water mites (Acari) were eaten only by C. bairdi.

Fall overlap values were significant for only one of the pairs that were tested: mature C. bairdi-immature C. bairdi (Table 12). Adult C. bairdi and immature C. bairdi showed almost no overlap with adult C. girardi, and that between adult C. girardi and immature C. girardi was the lowest recorded in any season for an intraspecific pair.

Summary of Food Habits

Benthic insect larvae were the main food items of both Cottus bairdi and Cottus girardi in Naked Creek, Virginia. Despite the overall similarity of the diets of these two species, however, several differences with regard to given food items were evident. My data for immature fish probably present a fairly accurate picture of the diets of these two sculpins when they are less than 45 mm SL, but that for mature fish must be

TABLE 12

FALL DIET OVERLAP (D) BETWEEN COTTUS BAIRDI AND COTTUS GIRARDI.

ABBREVIATIONS FOR SPECIES AND SIZE GROUPS AS IN TABLE 6.

	ab	ib	ag
ab	--	--	--
ib	.87	--	
ag	.09	.09	--
ig	.41	.42	.37

considered tentative in many cases (especially for C. girardi) due to small sample size.

Diptera was the most important order of insects in the diet of C. bairdi and one of the two most important orders in the diet of C. girardi. The most important family of dipterans in the diet of both species was Chironomidae. C. bairdi used these larvae most heavily in spring, while C. girardi used them most heavily in summer. In fact, the data indicate that this family was more important to C. bairdi than to C. girardi in all seasons except summer. The only consistent intraspecific pattern in the use of chironomids was in the fact that immature C. girardi used them more than did adults. Members of the suborder Brachycera were important food items only in winter and spring. In general, these fly larvae were more important to C. bairdi (especially males) than to C. girardi. One family of brachycerans that was somewhat important as a winter food, Dolichopodidae, was eaten only by C. bairdi. The most important family in this suborder, Empididae, was eaten by both species but was somewhat most important (by all measures) to C. bairdi. Tipulids (suborder Nematocera) were eaten by both species in small numbers but were most important to C. girardi in all seasons except spring. Among the less frequently eaten groups of dipterans, heleids and muscids were eaten only by C. girardi.

Ephemeropterans were probably the most important food for C. girardi and definitely the second most important food for C. bairdi. Much of the overall difference in percentages (especially in terms of numbers) for this order between C. girardi and C. bairdi was due to the much larger numbers

of chironomids in C. bairdi stomachs and not to great differences in numbers of mayflies eaten by the two sculpins (see Fig. 6). Ephemerellidae, the most important family of mayflies in the diets of both fish, were only eaten frequently in spring. Overall, this family seemed more important to C. girardi, but statistical tests on several dates indicated that C. bairdi had eaten significantly larger numbers of these larvae. The overall difference between species was, however, affected by the relatively greater importance of ephemerellids in the diet of adult C. girardi (this group was not generally useable in statistical tests because of small sample sizes). Ephemerellid consumption peaked in April for C. bairdi and in May for C. girardi perhaps indicating that the two fish species were using two different ephemerellid species that reached their peak abundance at different times. Tricorythids also seemed more important to C. girardi overall. Again, this difference seems to be mainly due to greater use by adult C. girardi (especially males). The peak occurrence of this food item was in August for both species. Heptageneidae and Siphonuridae were of similar overall importance to both sculpins. C. bairdi, however, ate many more heptageneids than did C. girardi in July (the peak month for this family), and adult C. girardi never ate many of these mayflies. Also the greatest usage of siphonurids was in April for C. girardi and June for C. bairdi. The spring peak in usage for C. girardi was mainly the result of relatively large numbers of unidentified siphonurids (those not identifiable beyond family) being eaten by immature C. girardi. The summer peak for C. bairdi was again mainly due to unidentified siphonurids (mostly in males). Genera identified include Isonychia,

Ameletus, and Siphonurus, but only Isonychia was of much importance. This genus occurred in female C. bairdi and immatures of both species primarily in spring and summer and was more important in the diet of the immatures. Small unidentifiable ephemeropterans were sometimes important food items, and they were more important in C. girardi than in C. bairdi. This trend is especially noticeable in immature C. girardi in February. Finally, two of the infrequently eaten families of mayflies, Leptophlebiidae and Potamanthidae, were eaten only by C. girardi.

The third most important order or insects in the diets of both species was Trichoptera. Hydropsychids were eaten more consistently by C. bairdi throughout the year, but, again, both species showed peaks in the usage of this prey in different months (July for C. bairdi and September for C. girardi). Male C. girardi were the only fish that ate no hydropsychids. In contrast to the other food items considered, most hydropsychids were keyed to one of two genera, and both of these were eaten in moderate to large numbers. Cheumatopsyche was eaten by all three groups of C. bairdi plus immature C. girardi, but was most important to male and immature C. bairdi. All three groups of C. bairdi plus female C. girardi ate Hydropsyche. Female and immature C. bairdi used this genus most extensively, and its use by all three groups of C. bairdi was mostly during summer. Female C. girardi ate relatively more hydropsychids than any other fish group in fall. This trend, however, is based on only two fish, and one of them had eaten an unusually large number of Hydropsyche. Hydroptilids were used to a similar degree by both species. Most of these caddisflies were also assignable to genus, and the most

important genus was Hydroptila. Overall this genus was most important in diets of males and immatures among C. bairdi and females and immatures among C. girardi. Once again, the groups eating relatively more of these prey changed from season to season. These groups were male and immature C. girardi in spring, male and immature C. bairdi plus female C. girardi in summer, and male C. bairdi in fall. The genus Oxyethira appeared only in immature C. girardi stomachs, and it appeared there in moderate numbers in summer. There were also several uncommon families in the diet of C. bairdi which did not occur in that of C. girardi. These included Glossosomatidae, Leptoceridae, Lepidostomatidae, and Odonoceridae. All of these but Lepidostomatidae occurred in immatures, and Lepidostomatidae and Leptoceridae occurred in males.

Two seasonally important prey items were utilized to different degrees by these two sculpins. Gastropods were most numerous in gut contents in summer and fall and were more important in C. bairdi. This prey occurred in C. bairdi during four months and in C. girardi during only one month. Also, the genera Physa and Lioplax along with the family Planorbidae occurred only in C. bairdi. Within C. bairdi, snails seemed more important to adults. Copepods (mainly winter and spring food items) were more important in immature C. girardi than in any other group. Adult C. girardi, however, utilized copepods very little as food.

In addition to the preceding groups, several less important gut items were either present in only one species or obviously more common in one species than in the other. Hydra sp., planarians, crayfish, four families of beetles, and one family of stoneflies were eaten only by C. bairdi,

while amphipods and fantail darters (Etheostoma flabellare) were eaten only by C. girardi. Nematodes appeared fairly commonly in stomachs during some seasons but were almost entirely restricted to the diet of C. bairdi. Conversely, oligochaetes were common food items in some months and were almost entirely restricted to the diet of C. girardi (males and immatures). Also, vascular plant debris was generally more common in C. girardi.

Two general trends were indicated in seasonal dietary overlap. First, the lowest overlap values in any given season were always between interspecific pairs. Overlap among the groups of C. bairdi was always greater than the arbitrary significance level ($D = 0.60$). Males and females usually overlapped the least in diet of any of the C. bairdi pairs. Within C. girardi, two pairs in summer had overlap values that were just below the significance level, and one pair in fall had a value that was well below this level. The three C. bairdi groups usually showed similar degrees of overlap with C. girardi. Among the groups of C. girardi, males (at least in spring and summer) showed the largest degree of overlap with C. bairdi, and females showed the smallest. The second general trend is that overlap was greatest in spring and summer and least in fall and winter.

CURRENT PREFERENCES

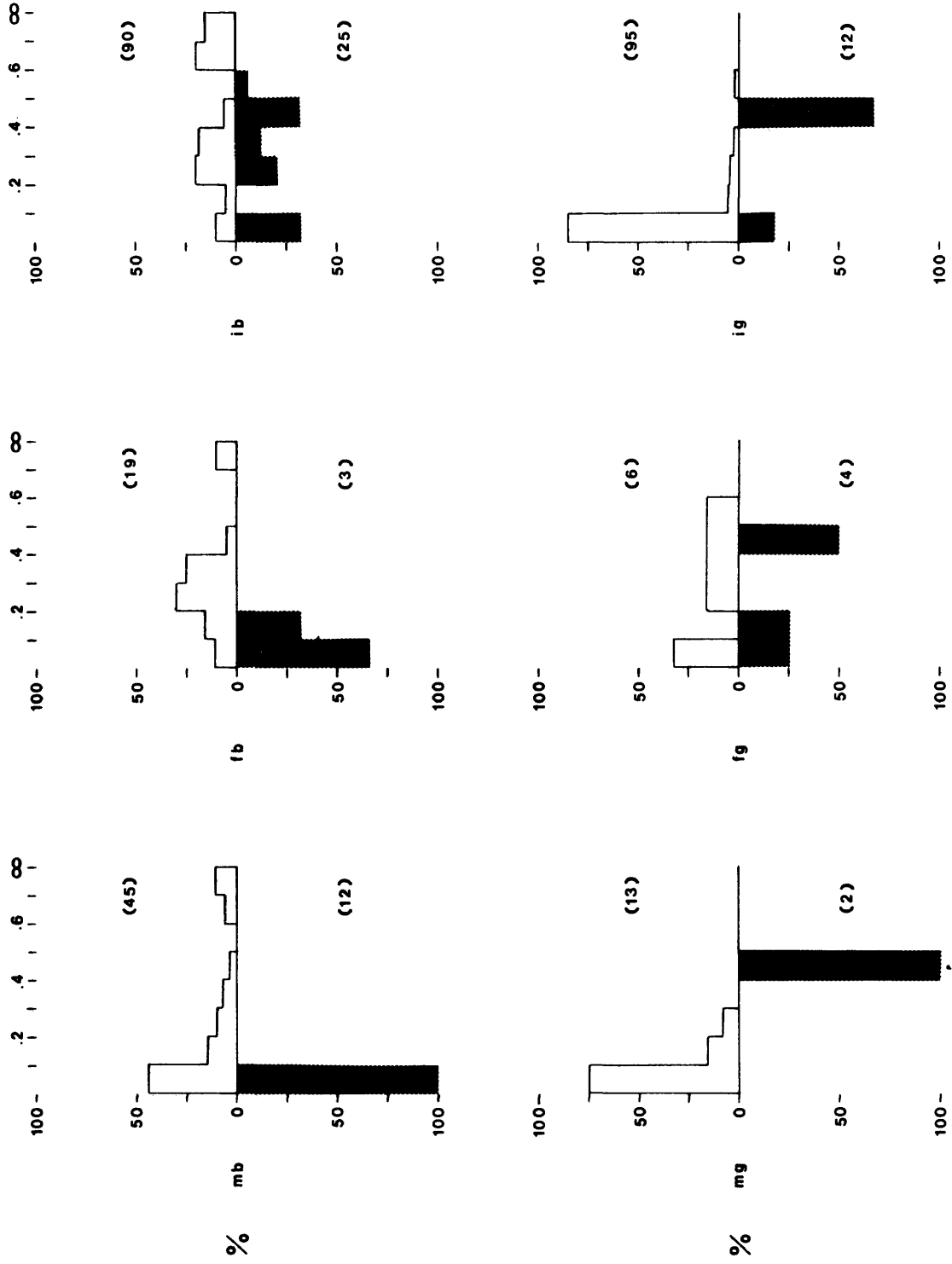
Cottus bairdi and C. girardi showed marked differences in current preference. Estimated current speeds were recorded for the area of capture of 194 C. bairdi and 132 C. girardi. The mean current speed for C. bairdi was 0.28 m/s and varied seasonally from 0.20 in winter to 0.38 in fall. The mean for C. girardi, however, was 0.07 m/s and ranged from 0.00 in fall and winter to 0.10 in spring.

Changes in current preference with changes in fish size were indicated by Spearman's coefficients of rank correlation between SL and current speed for both species. The values of this coefficient for C. bairdi and C. girardi, respectively, were -0.3819 ($p = 0.001$, H_0 : there is no correlation between SL and current speed) and 0.1552 ($p = 0.073$). In other words, as C. bairdi increased in length the current speed at which it occurred decreased significantly. The opposite was true of C. girardi, but the relationship was not quite significant at the 0.05 level.

Frequency distributions of the different size and sex classes of each species at various current speeds indicated a more complex situation than did the above comparisons (Fig. 11). The overall trends between species were mostly based on immature fish and on fish from Stations 2 through 6 due to large sample sizes in these groups. Eighty-nine percent of the immature C. bairdi at Stations 2 through 6 were found in areas with

Fig. 11. Percentages of Cottus bairdi and Cottus girardi found at various current speeds. Open bars indicate Stations 2 through 6 and shaded bars indicate Stations 1 and 7. Abbreviations for species and size groups as before. Numbers in parentheses are sample sizes.

Current Speed, m/s



slow to fast current, while 84% of the immature C. girardi at these stations were found in areas with no detectable current. Female C. bairdi exhibited a distribution at these stations that was similar to that in immatures, but males were more heavily concentrated in areas with no current (dead areas). Among C. girardi at Stations 2 through 6, males were similar to immatures in current preference, while females were more common at faster current speeds (the small sample in the latter case makes the conclusion quite questionable).

Some explanation is necessary of why Stations 1 and 7 were separated from the others in these comparisons. Robins (1954, 1961) states that C. girardi is generally more tolerant of warmer downstream conditions than is C. bairdi, and Andreasson (1969a) finds that C. poecilopus occurs in a wide variety of habitats upstream of the range of C. gobio but is confined to areas of slower current whenever the ranges of the two species overlap. These facts led me to believe, a priori, that the habitat preferences of C. bairdi and C. girardi might differ in different areas of the stream. Stations 1 and 7 represent the downstream and upstream limits, respectively, of my sampling in Naked Creek. I do not know, however, if they do or do not represent the extremes of the ranges of either species of sculpin. It was obvious from my data (Fig. 11) that the current preferences indicated for each species at these two stations were quite different from those indicated at the other five stations. Unfortunately, the small sample sizes at Stations 1 and 7 prevented further analysis of the data. Also, such analysis would be misleading since almost all fish from Station 1 came from areas of strong current, while

most of those from Station 7 came from areas of weak or no current. Applying this information to Fig. 11 indicates that C. bairdi was most common at Station 7 and that C. girardi was most common at Station 1. Detailed comparison of the habitat preferences of C. bairdi and C. girardi in isolation from one another must await further data. Accordingly, the remaining discussion of current preferences presented below does not include data from Stations 1 and 7.

Overlap values for current preference among the various groups of both species served to clarify the relationships mentioned above (Table 13). In addition to the rule-of-thumb used in dietary overlap evaluations, it was possible with most current comparisons to use chi square tests of the differences in current preference for each pair tested (H_0 : there is no association between fish group and current preference). Three pairs had overlap values greater than 0.60 and chi square probabilities greater than 0.05. Two of these pairs were intraspecific (female and immature C. bairdi and male and immature C. girardi), and one was interspecific (male C. bairdi and male C. girardi). At the other extreme, four pairs had overlap values of less than 0.40 coupled with chi square probabilities of less than 0.005. All four of these pairs were interspecific, and all four were combinations of either male or immature C. girardi with either female or immature C. bairdi. Both male C. bairdi and female C. girardi overlapped least with intraspecific groups and most with interspecific groups.

Two of the three groups of C. bairdi showed seasonal differences in current preference. Immature C. bairdi were found to differ significantly

TABLE 13

CURRENT PREFERENCE OVERLAP (D) AND CHI SQUARE PROBABILITIES OF THE ABSENCE OF DIFFERENCE IN CURRENT PREFERENCE (IN PARENTHESES) FOR COTTUS BAIRDI AND COTTUS GIRARDI FROM STATIONS 2 THROUGH 6. ABBREVIATIONS FOR SPECIES AND SIZE GROUPS AS BEFORE.

	mb	fb	ib	mg	fg
mb	--	--		--	--
fb	.51 (< .025)				
ib	.52 (< .005)	.72 (> .05)			
mg	.67 (> .05)	.34 (< .005)	.25 (< .005)		
fg	.54 (--)	.49 (--)	.52 (--)	.41 (--)	
ig	.57 (< .005)	.24 (< .005)	.24 (< .005)	.88 (> .10)	.41 (--)

($p < 0.005$) in current preference among the seasons of spring, summer, and fall (winter was not included in this test since all eight of the young C. bairdi taken in this season were from a current speed of 0.3 m/s). This fact does not, however, negate the above conclusions about immature fish since all immature C. girardi were in dead water in fall and winter ($n = 22$), and chi square tests for spring and summer between the two immature groups still revealed a significant difference ($p < 0.005$ in both cases). The seasonal difference in immature C. bairdi was due to the fact that over 50% of these fish were found in current speeds of 0.2 to 0.3 m/s in spring and summer, while 97% were found at speeds above or below this interval in fall (71% above and 26% below).

One might expect male C. bairdi to be found in faster current in spring than in other seasons since they showed an overall preference for slow current or dead areas but nested in flowing water. The percentages of these fish in dead water were 85% in winter, 9% in spring, 20% in summer, and 65% in fall. A chi square test revealed that the difference between spring and the other three seasons was indeed significant ($p < 0.005$). Therefore, in summer, fall, and winter the current preference of male C. bairdi probably overlapped more with those of male and immature C. girardi than is indicated in Table 13.

Sample sizes were too small to test for seasonal differences in male C. girardi or in females of either species.

As I mentioned earlier, time constraints on sampling sometimes made it necessary to classify current into one of three types instead of actually measuring its speed. These three categories were current, eddy, and dead.

Since current types were always recorded (regardless of whether or not current speed was measured), a larger sample size was available for each of the six fish groups when considering current type instead of current speed. Nevertheless, only one of the trends mentioned above is changed by using current type, and even this change is slight.

Out of 45 male C. bairdi for which current speeds were recorded, 44% were found in dead areas, while, out of 84 of these fish with recorded current types, only 23% were found in dead or eddy areas. I must point out, however, that an unknown percentage of these males could have been captured in areas with quite slow current (i.e., 0.1 to 0.2 m/s). Also, 41% of the male C. bairdi that were found in current were found there during the spring months.

Current type data did not conflict with current speed data in any of the remaining five fish groups, but it did reinforce the conclusion that was drawn from current speed data for female C. girardi. The sample size for these fish was 6 for current speed and 12 for current type. As noted above, this group seemed to occur in running water more often than did male or immature C. girardi. Accordingly, 83% of the female C. girardi with recorded current types were found in running water (44 and 25% for male and immature C. girardi, respectively).

MISCELLANEOUS HABITAT PREFERENCES

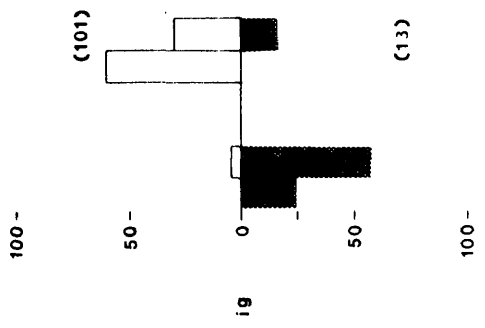
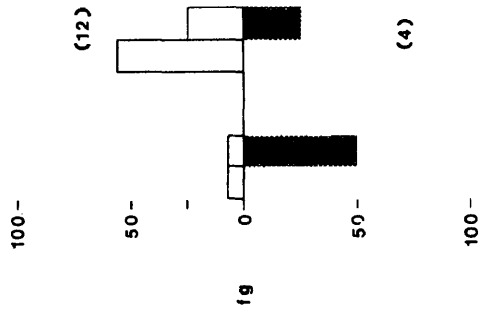
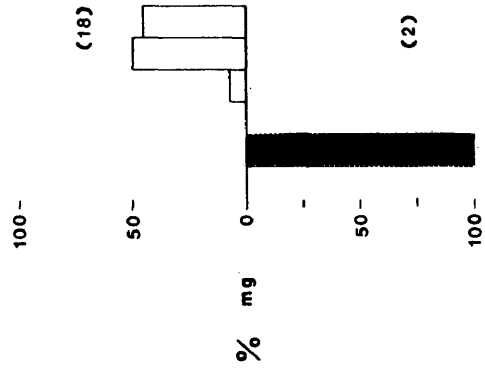
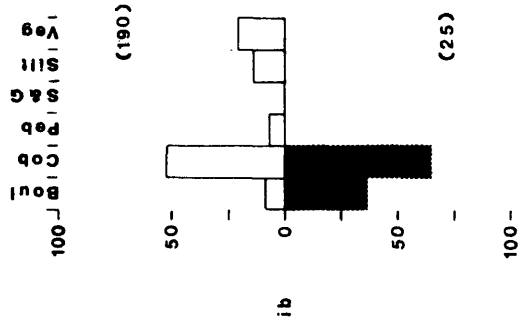
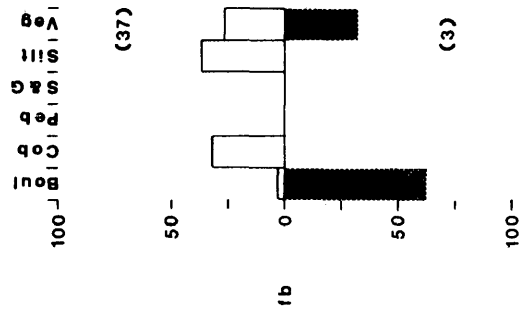
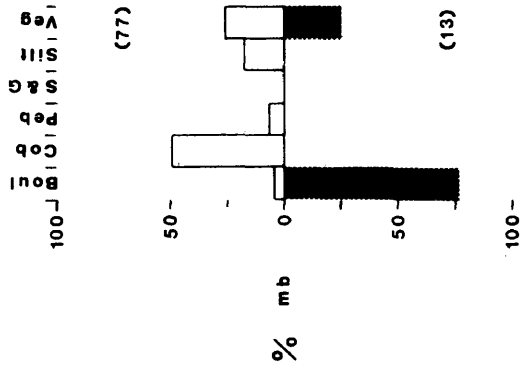
Other habitat data of interest that were recorded for each area of capture include substrate type, depth, and distance from shore. In general, I would expect these data to be correlated with current data since the slower current or dead areas that I sampled were usually deeper, closer to shore, siltier, and more likely to contain aquatic vascular plants than were those areas with faster current.

A marked difference was detected between C. bairdi and C. girardi in preferred substrate type (Fig. 12). At Stations 2 through 6 all three groups of C. bairdi were more commonly found on clean rock substrates (boulder, cobble, and pebble) than were any of the groups of C. girardi. Conversely, at these same stations, C. girardi was more common than C. bairdi (all three classes considered) on silt-covered substrates. Percentages of fish in vegetation were quite similar for all groups, but these data are misleading since most of the C. girardi and none of the C. bairdi in this category were found in beds of vascular plants. The trends were not the same at Stations 1 and 7, but no sculpins were taken from silty areas at either station, and the sample size was small.

Intraspecific variation in substrate preferences at Stations 2 through 6 was also noticeable for both species. The percentage of female C. bairdi on silty substrates was more than twice that recorded for either males or immatures. Male C. girardi never occurred on boulder or

Fig. 12. Percentages of Cottus bairdi and Cottus girardi found on various substrate types. Open bars indicate Stations 2 through 6 and shaded bars indicate Stations 1 and 7. Abbreviations for species and size groups as before. Numbers in parentheses are sample sizes.

Substrate Type



cobble, whereas small percentages of both females and immatures were found in such areas. Also, about 15% more of the male C. girardi occurred in vegetation than did females or immatures.

Overlap in substrate preference (Table 14) was always significant (≥ 0.60) between intraspecific pairs and, except for those pairs involving female C. bairdi, was always non-significant (< 0.60) between interspecific pairs. Thus, it seems that these six categories of fish were divided into a soft substrate group which included all C. girardi plus a firm substrate group which included male and immature C. bairdi. Female C. bairdi were intermediate between these two groups.

At Stations 2 through 6 all groups of C. girardi demonstrated a tendency to live in deeper water than did the corresponding group of C. bairdi (Fig. 13). The only depth (out of those containing at least 5% of any group) at which the percentage for C. bairdi was higher than that for C. girardi was 0 to 10 cm. Within each species mature fish were generally in deeper water than immatures, and males were generally in deeper water than females.

At Stations 1 and 7 the interspecific and intraspecific trends in depth preference were similar to those at Stations 2 through 6 despite the small sample sizes. The only marked exception was the difference between sexes in both species.

Finally, an obvious interspecific difference was also found in the distance from the nearest shore for areas of capture of these two sculpins (Fig. 14). At Stations 2 through 6 percentages of all groups of C. girardi at 2 m or less from shore were higher than those for any group of C.

TABLE 14

SUBSTRATE PREFERENCE OVERLAP (D) FOR COTTUS BAIRDI AND COTTUS GIRARDI FROM STATIONS 2 THROUGH 6. ABBREVIATIONS FOR SPECIES AND SIZE GROUPS AS BEFORE.

	mb	fb	ib	mg	fg
mb	--	--	--	--	--
fb	.77	--			
ib	.93	.70	--		
mg	.42	.68	.35	--	
fg	.54	.75	.51	.76	--
ig	.47	.70	.40	.79	.89

Fig. 13. Percentages of Cottus bairdi and Cottus girardi found at various depths. Open bars indicate Stations 2 through 6 and shaded bars indicate Stations 1 and 7. Abbreviations for species and size groups as before. Numbers in parentheses are sample sizes.

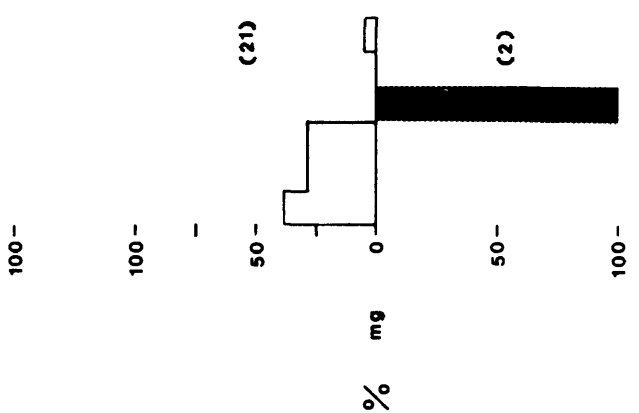
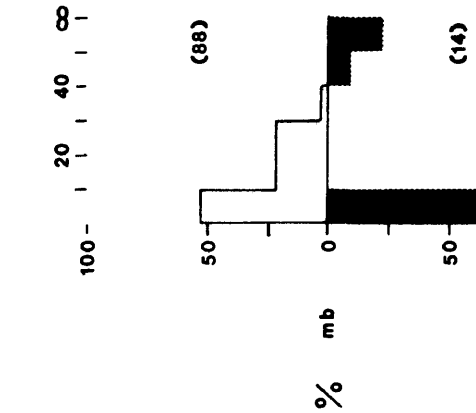
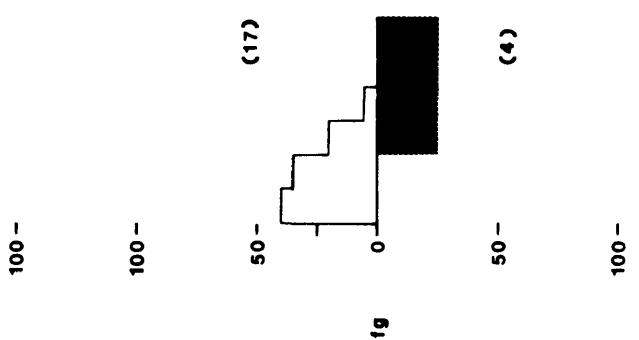
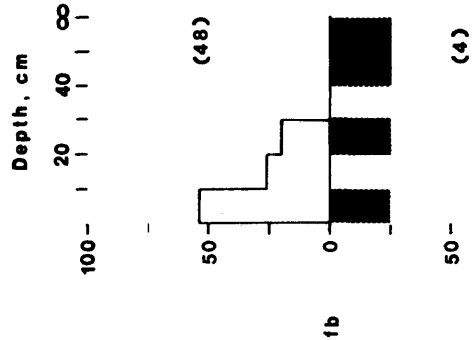
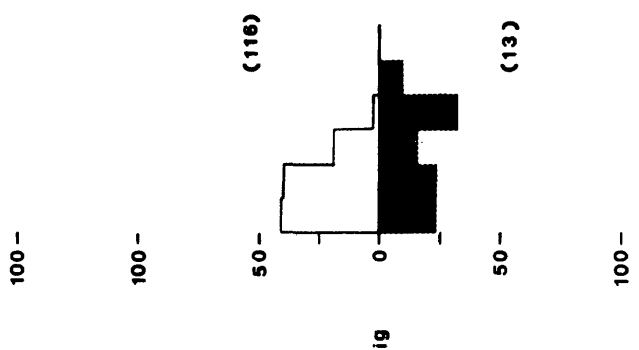
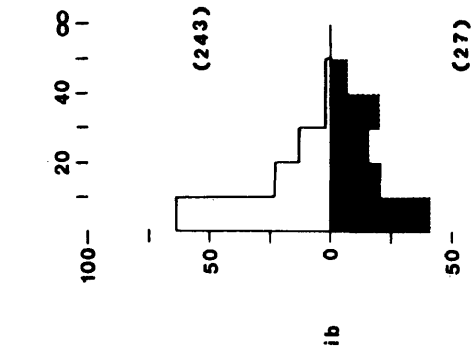
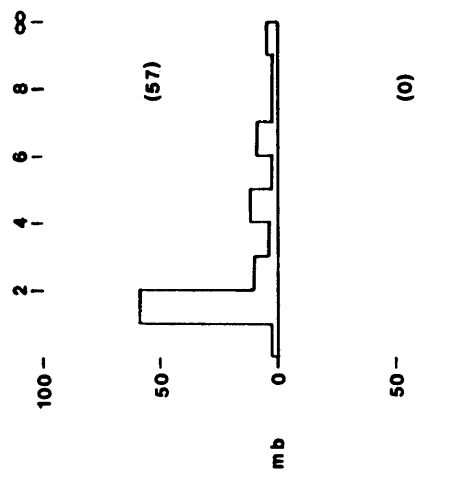
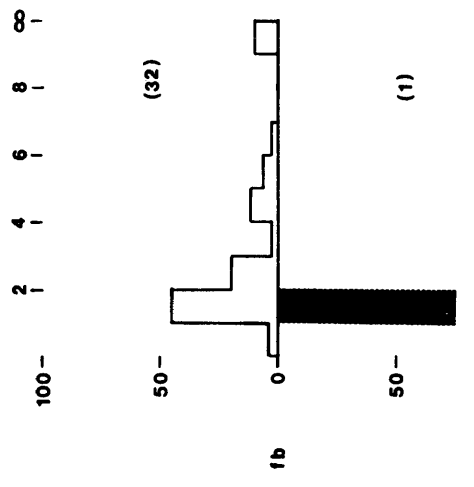
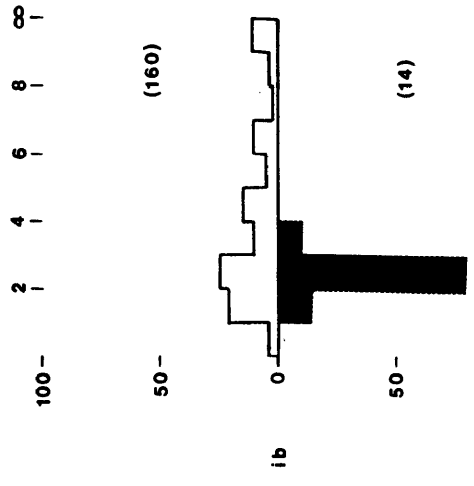
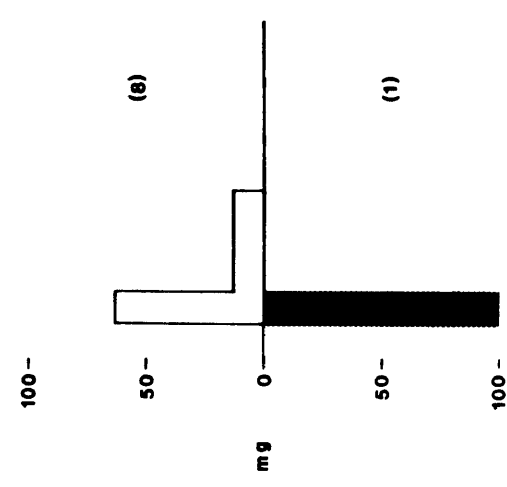
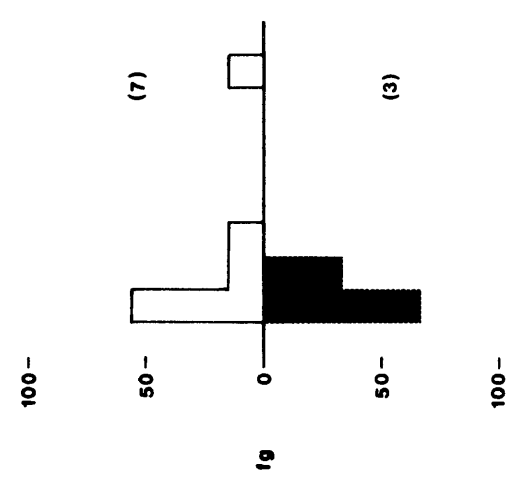
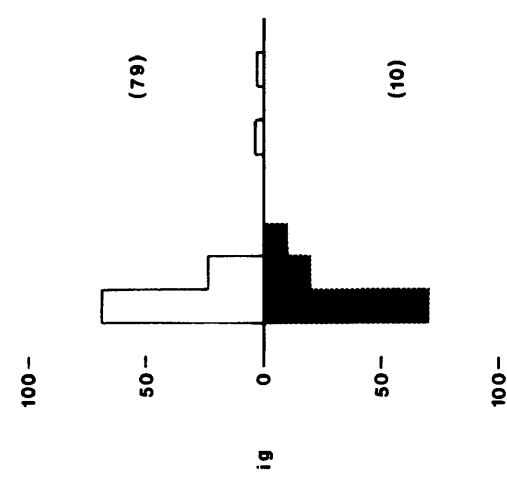


Fig. 14. Percentages of Cottus bairdi and Cottus girardi found at various distances from the nearest shore. Open bars indicate Stations 2 through 6 and shaded bars indicate Stations 1 and 7. Abbreviations for species and size groups as before. Numbers in parentheses are sample sizes.

Distance from Shore, m



%



%

bairdi. This difference was especially marked between immature fish. At Stations 1 and 7 only the immature sample sizes were reasonably large, and the trend for these fish was the same as at Stations 2 through 6.

Intraspecific differences in distance from shore were only marked in C. bairdi at Stations 2 through 6. Male C. bairdi were much more likely to be found at 2 m or less from shore than were immatures. Female percentages were intermediate between those of the other two groups.

DISCUSSION

Several ecologically important differences between Cottus b. bairdi and Cottus girardi were evident in Naked Creek. First, C. girardi was larger than C. bairdi through at least the first summer of life and may reach a larger maximum size. Accordingly, female C. bairdi matured at a smaller size than did female C. girardi. C. bairdi nests under rocks in flowing water during March and April. No definite C. girardi nests were found, and mature individuals were conspicuously absent from samples taken during the probable breeding season (February and March). Habitat segregation was quite marked in regard to current and substrate. Finally, the overall diets of both species were quite similar, but differences did exist in the relative importance of some food items. Some of these differences may be related to the ecology of these two species (or their relatives) when they are allopatric, and some may be related to competition that occurred after they became sympatric.

The observed size differences in young-of-the-year fish could indicate faster growth, larger size at hatching, or earlier spawning for C. girardi. I have no evidence in regard to the first two possibilities, but I feel that some discussion of spawning habits is needed in regard to the third possibility. Eggs of C. bairdi have been found from late winter to early summer. My records from March and April are, therefore, not surprising. Some of the recorded dates include February to May in Utah

(Zarbock 1952) and Wyoming (Simon and Brown 1943), April in Ohio (Downhower and Brown 1977) and Michigan (Hann 1927), April to May in Wisconsin (Ludwig and Norden 1969), and June to July in Montana (Bailey 1952). Savage (1963) discovered the egg clusters of Potomac drainage sculpins on March 11, but, as I mentioned above, the specific identity of his specimens is in question. Most descriptions of spawning sites are similar to mine in that eggs are found on the underside of rocks in current. Bailey (1952) did, however, find some nests in dead areas, and Ludwig and Norden (1969) found some nests under rocks in silty areas, two attached to Elodea sp., and two in tunnels in packed loam. The only spawning data for C. girardi is one male which Robins (1954) says was "in spawning condition" when taken on April 10 in Virginia.

Perhaps my inability to find C. girardi nests indicates that this fish spawns in a manner similar to that of its widespread relative, C. carolinae. The literature contains many records of C. bairdi nests, but I have found no records of C. carolinae nests. Craddock (1965), in the one major life history study of C. carolinae, reports that no nests could be found. He does, however, infer that breeding occurred from January to March (with a peak in February) based on the occurrence of ripe males and females during this period. Post-larvae and juveniles appeared in March and April in a cave entrance where there was little current and an abundance of roots and debris. Egg shells were also found attached to stones or roots in this area. As in the present study, males disappeared during the spawning season. Based on this information, Craddock postulates that C. carolinae spawns under undercut banks or waterfalls or lateral to the

main channel in springs or perhaps crayfish burrows. Furthermore, he compares his data with information on C. bairdi and concludes that C. carolinae is larger at maturity (91 to 105 mm total length or approximately 75 to 90 mm SL for females) and lays a larger number of eggs. Other data on C. carolinae includes Robins' (1954) statements that the examination of ovaries of C. c. carolinae indicated fall spawning and that C. c. carolinae taken "with breeding groups of various forms of the bairdi complex" were not in breeding condition. The same author does, however, mention that C. c. zopherus (the form most closely allied to C. girardi) seems to breed in March or April. Small (1975) postulates winter spawning for C. carolinae in Kentucky because young less than 20 mm in length were found in April and May. Williams and Robins (1970) also failed to find the nests of C. c. infernatus. These authors postulate that members of the C. carolinae group lay eggs singly or broadcast them instead of building nests. They also mention that these sculpins contain larger numbers of eggs than do members of the C. bairdi group.

Based on my data plus the work of the above mentioned researchers, I would postulate that C. bairdi and C. girardi do not compete directly for breeding sites. Young of both species were first found in May, but those of C. girardi were markedly larger than those of C. bairdi. This size difference may indicate that C. girardi spawns earlier than C. bairdi. Among my samples, female C. girardi consistently contained larger ova in September and November, but this could be an indication of larger egg size at the time of spawning. Also, the sample sizes of mature female C. girardi in these two months were quite small. Perhaps more

importantly, the spawning habitat of these two species is probably different. My failure to find nests plus the scarcity of mature C. girardi in late February and March may indicate secretive spawning habits for this species much like those postulated for C. carolinae.

In a review of resource partitioning in ecological communities, Schoener (1974) states that habitat dimensions are often more important than any others in separating species. Competition for living space between these two sculpins is minimized by several factors at most of the stations sampled. Two groups of fish can be defined on the basis of current preference. Female and immature C. bairdi generally occurred flowing water, while male and immature C. girardi generally occurred in dead or eddy areas. The differences between these two groups were significant. Female C. girardi approached the first group, but sample size was problematical in these fish. It seems likely that their primary habitat was one that I could not sample effectively with seine or dipnet (e.g., deeper pools and runs). Male C. bairdi approached the second group, but the pattern was complicated by a movement to flowing water in spring (presumably to spawn). Nevertheless, no difference was detected in current preference between male C. bairdi and male C. girardi. Within the first group, female C. bairdi were relatively more common than immatures in areas with silt or algae covered substrates. The silty areas were not dead areas like those often inhabited by male and immature C. girardi but were areas lateral to the main current where slowly moving water allowed some silt to accumulate. In association with this trend, females generally occurred closer to shore. Female C. girardi also showed a

preference for silty areas and generally occurred in deeper water than did either female or immature C. bairdi. Within the second group, male C. girardi were relatively more numerous in beds of vegetation and in deeper water than were immatures. Male C. bairdi preferred less silt and shallower water than did either of these two C. girardi groups.

There is an abundance of literature suggesting that Cottus species are usually widespread when alone but become habitat specialists when in sympatry with a congener. Andreasson (1969a) comments on the habitat preferences of C. poecilopus and C. gobio in Europe. C. poecilopus generally occurs higher in streams than does C. gobio, and, above the upper limit of C. gobio's range, C. poecilopus occurs in a wide variety of habitats. In areas where their ranges overlap, however, C. poecilopus is confined to slow current or reservoirs, while C. gobio occurs in large tributaries in a strong current. In a later study Andreasson (1972a) indicates that the effects of these two species upon one another change in different parts of their ranges. C. gobio displaces C. poecilopus to upstream areas in southern and middle Sweden but not in northern Sweden. He attributes this difference to the fact that C. poecilopus occurs in current more often in the northern part of its range. A similar pattern is seen in C. aleuticus and C. asper in British Columbia (Mason and Machidori 1976). In areas of co-occurrence large C. asper are found in deep pools and under log jams and undercut banks. Intermediate sized C. asper and large C. aleuticus are found in these same areas but at shallower depths. Small and intermediate sized C. aleuticus occur in riffles. Finally, subyearlings of both species live in intertidal riffles, but C.

asper is in deeper areas than is C. aleuticus. In upstream areas populated only by C. aleuticus, however, this species occurs in a wide variety of habitats including those dominated by C. asper downstream. Moyle (1976) notes similar interactions between C. perplexus and C. gulosus and other species of Cottus.

Studies dealing with stream-dwelling C. bairdi alone indicate that this species occupies a wide variety of habitats but probably prefers clean rock substrates in flowing water. Anderson (1975) reports that Illinois C. bairdi preferred riffles with rocky substrates and clumps of algae in the main channel of the stream. In Montana older sculpins were most abundant in riffles with rocky substrates and (at one station) in beds of aquatic vascular plants. They were usually absent from pools with sand or clay substrates, but a few occurred in quiet, shallow water near shore (Bailey 1952). In their Wisconsin study Ludwig and Norden (1969) found C. bairdi most often in areas with rubble substrates and moderate current, but sculpins were also plentiful in Elodea beds. They could find few of these fish, however, over silt or sand in areas without rooted vegetation. Finally, Zarbock (1952) found Utah C. bairdi to be most abundant over coarse gravel and small rocks. The habitat of sculpin fry is described by Bailey (1952) and Hann (1927). The former author found young fish (< 20 mm total length) to be most abundant in shallow, slow water where they could hide by stirring up silt and allowing it to settle over them. In contrast, the latter author found C. bairdi fry over smooth pebble bottom. Habitat partitioning by sex has only been noted by Bailey (1952). He noted no segregation of the sexes during most of the

year. During the breeding season, however, males were nesting in deeper water, and females were confined to shallower areas.

The habitat preferences of C. girardi in the absence of other sculpins are unknown, but some data is available for C. carolinae. Craddock (1965) notes that young-of-the-year C. c. carolinae occurred in eddy and slow current areas with substrates of debris and detritus. These young fish were also common in beds of aquatic plants. Adults were usually found at the edge of current and were often associated with large boulders. Some also occurred everywhere from riffles to pools plus beds of aquatic plants. The upper ends of pools in moderately flowing water consistently contained the largest specimens. The very general information provided by Robins (1954) and Williams and Robins (1970) does not conflict with that provided by Craddock (1965). Further studies are obviously needed to determine whether or not C. girardi and C. carolinae have similar habitat preferences. There is apparently, however, little difference in the habitat preferences of C. bairdi and C. carolinae when each occurs alone except for the possibility that C. carolinae is more tolerant of pool conditions.

Some literature also exists concerning how C. bairdi reacts to the presence of other sculpins. Robins (1961) discusses the ecological incompatibility between C. bairdi and other members of the redbfin species group. When C. bairdi and C. cognatus occur in the same streams, C. cognatus is confined to grassy areas upstream, while C. bairdi takes the rocky, warmer downstream areas (sometimes including rivers). When C. bairdi and C. baileyi are in the same stream, C. bairdi is found in the

mainstream throughout the area, while C. baileyi is in scattered pockets. Thus, in these cases of sympatry with other redbins C. bairdi occupies the rockier habitats and the mainstream much as it does in Naked Creek.

Information on the interaction between C. bairdi and members of the C. carolinae species group is quite scarce and general. Robins (1954) notes that members of the C. carolinae group tolerate warmer temperatures than do members of the C. bairdi group when they are sympatric. Also, C. carolinae group fish are more wide-ranging in such areas. The same author was unable to find any ecological separation between C. c. kanawhae and sympatric C. bairdi or between C. girardi and sympatric C. bairdi. As I mentioned previously, however, he found C. bairdi to be restricted to cold headwater streams, while C. girardi is more adaptable and occurs from headwaters downstream to warmer brooks. Armstrong and Williams (1971) found C. carolinae to be more widespread in the area of the south bend of the Tennessee River than was C. bairdi. Furthermore, C. bairdi was generally confined to colder water areas, especially springs. In the main channel of the New River C. carolinae is quite common, whereas C. bairdi is extremely rare (Hocutt et al. 1973). Thus, the overall distribution of C. girardi and C. bairdi in the Potomac drainage [as described by Robins (1954)] probably parallels that of C. bairdi and other members of the C. carolinae species group in other drainages. Little is known, however, about the respective habitats of these two groups in their areas of overlap.

Similarly, food habits studies of these two groups have only been done in areas of allopatry. The preponderance of benthic insect larvae

in the diet of C. bairdi in Naked Creek is not surprising based on the data from other studies of stream dwelling populations of this species. In New York, Koster (1937) found C. bairdi to contain mostly Diptera, Ephemeroptera, and Trichoptera, while Daiber (1956) found them to contain mostly Diptera, Trichoptera, and Plecoptera. Dipterans, ephemeropterans, trichopterans, and amphipods were found to be the most important foods in a Minnesota study (Dineen 1951). In Montana, Bailey (1952) again found the most important items to be Diptera, Trichoptera, and Ephemeroptera. Finally, Zarbock (1952) found that Trichoptera, Ephemeroptera, and Plecoptera were the dominant items in Utah.

Somewhat different food habits for C. bairdi are presented by Anderson (1975) and Walker (1975). Working in Illinois, the former author found Isopoda to be the most important food group followed by Diptera and Trichoptera. This study was, however, based on fish collected on one day and at one station, and the results might, therefore, represent a seasonal or local phenomenon. Walker (1975) compared food items in Pennsylvania sculpins by using an "Index of Relative Importance" based on percent numbers, percent calories, and percent frequency of occurrence. By this method crayfish, other C. bairdi, simuliids, and chironomids were found to be the most important foods. Unlike the first author, Walker (1975) had large sample sizes, and he sampled over an extensive period of time.

Since there are no previous studies of the food habits of C. girardi, I can, once again, only compare my data with that from studies on C. carolinae. Small (1975) found C. carolinae in Kentucky to be eating

mostly isopods, amphipods, chironomids, baetids, and coleopterans. Also working in Kentucky, Craddock (1965) found that crustaceans, fish, and insects were all important food items for this sculpin. Furthermore, he compares his data with that from studies (mainly those that I mentioned above) of C. bairdi and concludes that the typical C. carolinae diet would include more crustaceans (decapods, amphipods, and isopods), more fishes, and fewer insects than would the typical C. bairdi diet.

Comparing my data to that of Craddock (1965), neither C. bairdi nor C. girardi approaches C. carolinae in the use of either crustaceans or fish: isopods were not eaten by either species, amphipods were eaten only by C. girardi and were extremely rare, decapods were eaten only by C. bairdi and were also rare, and fish were eaten by both species and were rare. It is interesting to note, however, that one of the food differences between these two sculpins in Naked Creek would have been predicted based on Craddock's work. This is the fact that small crustaceans, copepods in this case, were more important to C. girardi than to C. bairdi. It is especially unfortunate in this instance that I was able to collect so few large C. girardi (> 45 mm SL). Craddock's C. carolinae fed largely on Diptera, Ephemeroptera, Isopoda, and Amphipoda when approximately 45 mm or less in SL. Above this size, however, insects began to decrease in importance, while decapods and fish began to increase. This trend is especially marked in fish of about 65 mm SL and greater, and I captured very few specimens in this size range.

The diets of C. bairdi and C. girardi may not be as similar as my data suggest due to the level of taxonomic resolution that was possible

for different food groups. For example, the family Chironomidae was a major food group for both species of sculpin, but I do not know what genera or species of chironomids the two fish were eating. I was only able to identify one genus of chironomids. Most of the hundreds of these larvae that I found in sculpin stomachs were keyed to family only. Straskraba et al. (1966) found that C. poecilopus and Phoxinus phoxinus were both feeding heavily on chironomids, but a closer look at their data reveals that there was actually no dietary overlap in this area because the genera being consumed by the two species were completely different. Furthermore, it is probably safe to assume that there are many species of chironomids available as sculpin food in Naked Creek. A body of water may support anywhere from a few to as many as 60 species of these insects, and more than 30 species have been reported from productive areas of streams (Pennak 1978). In a detailed ecological study of Doe Run in Kentucky, Minckley (1963) was able to identify 15 species of chironomids and suggests that there were probably many more that he did not find or could not identify. Similarly, at least three species of Ephemerella occurred in Naked Creek because I was able to identify three different subgenera. Unfortunately, however, relatively few of the Ephemerella in fish stomachs were identifiable to subgenus, and most of those that were identifiable were in the subgenus Ephemerella. A similar situation exists regarding the mayfly families Heptageniidae and Siphonuridae. It is also interesting to note that in two families whose members were usually keyed to genus, Hydropsychidae and Hydroptilidae, there were marked dietary differences between the two fish at the generic level that

were obscured at the family level. The generally high values that I have recorded for dietary overlap may reflect this lack of taxonomic resolution.

The fact that the peak usage of various food items by the different fish groups is often in different months may be due to the usage of more than one species within a food category or to some other factor. C. bairdi ate large numbers of chironomids in all months except July, August, and September. The only two months in which C. girardi ate more chironomids than did C. bairdi were July and August. Also, peak usage of these larvae occurred in April for C. bairdi and May for C. girardi. Similarly, C. bairdi used more ephemereids in April than in any other month, while C. girardi used more in May. Analogous situations existed in the usage of cladocerans, siphonurids, hydropsychids, and hydroptilids. It seems that such results could be explained by usage of different species that peaked in abundance at different times, by changes in the habitat of prey species during their life cycle, or merely by sampling error due to random local variations in prey abundance. Many aquatic insects (including ephemereids) move towards the banks of the stream when they are preparing to emerge (Hynes 1970). The same author also states that closely related species of Ephemerella often succeed each other temporally in streams.

In several cases the diets of the six groups of sculpins considered in this study are obviously related to their habitat preferences. Thorup (1964) states that the faunas associated with certain substrate types are well-defined and can be called communities. This is not an absolute division, however, since it is rare that a species will be totally absent

from other than its preferred habitat. Similarly, Cummins (1964) mentions the fact that areas with slower current (depositional areas) and areas with rapidly flowing water (erosional areas) each have a characteristic fauna with specific adaptations to the conditions in that area. Unfortunately, habitat diversity among members of several of the important prey taxa encountered in this study (e.g., Chironomidae and Ephemerellidae) precludes any comparisons of prey and predator habitats without extensive benthic sampling and further taxonomic resolution. Of the prey organisms found in Naked Creek sculpins, the following are usually characterized as flowing water specialists: Simulidae (Hynes 1970; Usinger 1956), Pseudocloeon (Edmunds et al. 1976), Isonychia (Edmunds et al. 1976; Minckley 1963), Glossosoma (Hynes 1970; Kovalak 1978), Hydropsyche (Minckley 1963; Wiggins 1977), and Cheumatopsyche (Wiggins 1977). Simulids and Hydropsyche were most important in the diet of the fast current fishes, immature and female C. bairdi. The former group was never eaten by adult C. girardi, and the latter was never eaten by male or immature C. girardi. Glossosoma was a relatively rare food item but was confined to the diet of immature C. bairdi. Cheumatopsyche was never eaten by adult C. girardi and was most important to male and immature C. bairdi. All three groups of C. bairdi used Pseudocloeon to a moderate degree as a food item. Only immatures among C. girardi used this food group, and they used it less than did any group among C. bairdi. Isonychia was never eaten by males of either species, but, surprisingly, these nymphs were used most heavily by immatures of both species. Thus, current dwelling insects were generally being eaten by current dwelling fish with the only

serious exception being Isonychia. Of the two fish that were intermediate in current preference, male C. bairdi often shared food items with the faster current fish, while female C. girardi shared only Hydropsyche with this group but did eat moderate numbers of these caddisflies.

Sculpin prey that are generally assigned to slow current and soft substrate areas include Oligochaeta (Minckley 1963; Pennak 1978), Cladocera (Pennak 1978), Copepoda (Pennak 1978), and Oxyethira (Wiggins 1977). Oligochaetes never occurred in females of either species and were definitely most important in the slow water fish, male and immature C. girardi. All three groups of C. bairdi and immature C. girardi ate copepods, and they were most important in immature C. girardi. On the other hand, this group also assumed a relatively important role in the diets of the fast current fish, female and immature C. bairdi, during certain months. Cladocerans were eaten in similar numbers by immatures of both species plus female C. bairdi. Oxyethira was eaten only by immature C. girardi. Thus, the burrowing oligochaetes and case-dwelling Oxyethira (Pennak 1978) were obviously most important in the diet of fish having habitat preferences similar to theirs. The comparatively frequent use of copepods and cladocerans by current-dwelling fish may be explained by the fact that these two groups of crustaceans are generally adapted for a planktonic existence in lentic habitats (Pennak 1978). Accordingly, they are not very dense and are poor swimmers. They are, thus probably more susceptible to being carried away by nearby currents than are oligochaetes and Oxyethira. Furthermore, if these copepods and cladocerans are among those that live in close association with debris and aquatic plants

(Pennak 1978), then the feeding activity of C. girardi near the edge of a dead area may dislodge them into the current where they are preyed upon by C. bairdi.

If differences in resource use between and within species (such as those that I have described in these two sculpins) are not just due to random variability but are indeed generated by competition, then they should fit into logical patterns (Schoener 1974). One such pattern that Schoener (1974) mentions is complementarity among niche dimensions. If more than one niche dimension is important in inter- or intraspecific ecological separation, then similarity along one dimension should imply dissimilarity along another. For example, competition would be minimized if animals that specialized in the occupation of the same habitat type used different foods within that habitat. Schoener (1974) gives examples from the literature for five combinations of niche dimensions for which complementarity might exist. I have already discussed complementarity in different habitat dimensions in these two sculpins, and my study contains data pertinent to at least one other type of complementarity.

Food type and habitat type have been shown to be complementary in some animals. Schoener (1974) lists examples of this phenomenon in birds, lizards, fish, and crustaceans. Werner et al. (1977) noted that largemouth bass, Micropterus salmoides, and bluegill Lepomis macrochirus, were unusual among the members of a mixed centrarchid community in that their preferred habitats were very similar. Their food habits were, however, markedly different. Also working with fish, Keast (1977) noted similar but intraspecific patterns in rockbass, Ambloplites rupestris,

and bluegill. In the former species, year classes differed in diets but not in habitats, while in the latter the reverse was true. As I indicated above, however, habitat and diet are probably not independent niche dimensions in these sculpins. In fact, Schoener (1974) notes that there are more cases in the literature where similarity along one niche dimension implied similarity along another than there are of complementarity. He further states that this fact is probably due to the recognition (on the part of the researcher) of dimensions that are not independent. Nevertheless, there are trends in my data that seem to indicate food-habitat complementarity. Male and immature C. girardi occupy quite similar habitats, but, mature males are obviously larger than immatures and should, therefore, be able to consume larger prey (unless mouth width reaches a maximum before maturity). Accordingly, small food items such as chironomids and copepods were more important in the diet of immature C. girardi than in that of males, while relatively larger (especially in cross section) ephemereids and tricorythids were more important in males. On the other hand, two relatively large good types that are generally more important in flowing water, Isonychia and Cheumatopsyche, were eaten only by immature C. girardi. Also, male and immature C. girardi overlapped more with each other in diet than they did with any other group except female C. bairdi. Among the groups of C. bairdi, males and immatures were most similar in substrate preference, while females and immatures were most similar in current preference. According to Bailey (1952) females should have narrower mouths than males and should, therefore, be in an intermediate position between males and immatures in this

character. The complex habitat division plus this complex size division makes the interpretation of any possible complementarity in C. bairdi quite difficult. Perhaps this is the reason that when one compares those items that are more important to the different groups of C. bairdi, a confusing mosaic of small and large items emerges. No consistent patterns were detected among these three fish groups in their use of their two most important food items, chironomids and ephemereids. This is despite the fact that one of these is a relatively small food item, and the other is a relatively large one. Some differences related to mouth width may be seen in the fact that the very small items Copepoda and Cladocera were most important in females and immatures, but then one must explain why hydroptilids and Cheumatopsyche were most important to males and immatures. Diet overlap values indicated that the two larger groups of C. bairdi, males and females, generally overlapped less with each other than they did with immatures, but intraspecific overlap values were never less than 0.66 in this species. It is obvious, therefore, that two groups of C. girardi inhabiting similar habitats do partition the available food, and that this partitioning may be related to mouth size. The trends in C. bairdi are confusing, but perhaps a study comparing actual food size (by measuring gut items) or comparing foods at the species level would be enlightening. It is also interesting in this regard that, although food differences do exist between the two immature groups, most of the major food types are shared.

In summary, Cottus b. bairdi and Cottus girardi in Naked Creek, Virginia do partition the available resources. Niche dimensions involving

habitat seem most important, but much work remains to be done on food size, food taxa, and possible temporal partitioning between these species. The ecology of these two fish in allopatry and in other areas of sympatry plus the spawning of C. girardi also remain to be studied.

APPENDIX A

DETAILS OF COLLECTING TRIPS TO NAKED CREEK

Date	Station	Nos. of Fish Taken		Comments
		<u>C. bairdi</u>	<u>C. girardi</u>	
9-21-75	6	3	2	
11-15-75	6	4	1	
4-24-76	5	16	0	
4-24-76	6	17	1	
5-22-76	5	5	0	
5-22-76	6	0	0	
5-23-76	5	5	1	
6-20-76	4	7	1	
6-20-76	5	11	8	
7-7-76	1	2	1	
7-7-76	2	0	6	
7-7-76	7	9	2	
7-25-76	4	15	5	
7-25-76	5	12	4	
8-14-76	1	1	1	
8-14-76	2	0	4	
8-15-76	4	2	6	
8-15-76	5	7	1	
8-15-76	7	18	2	
9-25-76	4	15	1	
9-25-76	5	16	2	
10-31-76	6	2	0	
11-1-76	4	25	8	
11-1-76	5	7	5	
11-1-76	7	0	0	Very few fish of any kind in area.
2-10-77	3	11	6	
2-10-77	4	20	4	Dead areas covered by ice with several species of fish (including both sculpins) underneath.
2-10-77	5	10	0	Stream almost completely frozen over. Collected from small open riffle area.

APPENDIX A (Continued)

Date	Station	Nos. of Fish Taken		Comments
		<u>C. bairdi</u>	<u>C. girardi</u>	
2-10-77	7	0	0	Stream mostly frozen over. Fish still scarce in area.
3-5-77	1	3	0	
3-5-77	2	1	8	
3-5-77	3	12	0	Two people searched for nests for 30 min. Searched from dead areas to riffles.
3-5-77	4			Two people searched for nests for 30 min. Searched from dead areas to riffles. No nests.
3-5-77	5	3	1	
3-19-77	3	13	8	Two people searched for nests for 15 min. Searched from dead areas to riffles. No nests.
3-19-77	4	16	9	Three people searched for nests for 20 min. Searched from dead areas to riffles. Two nests found in current. One guarded by male <u>C. bairdi</u> . No <u>C.</u> <u>girardi</u> in area of nests but many <u>C. bairdi</u> .
3-19-77	7	0	0	Fish still scarce in area.
4-16-77	4	24	10	Two people searched for nests for 20 min. Searched from dead areas to riffles. Nine nests found in current: 5 guarded by male <u>C. bairdi</u> . Only one <u>C.</u> <u>girardi</u> in nesting area but many <u>C. bairdi</u> .
4-16-77	5	8	6	
4-16-77	Unnumbered	0	0	One person searched with mask and snorkel for 25 min. in very deep area between stations 2 and 3. No nests or sculpins seen.
5-11-77	1	8	12	Two people searched for nests for 45 min. Searched from dead area to riffles. No nests.
5-11-77	2	0	7	
5-11-77	4	30	9	Two people searched for nests for 15 min. Searched from dead areas to riffles. No nests.
6-25-77	4	12	10	
6-25-77	5	13	5	
6-25-77	7	4	1	

APPENDIX A (Continued)

Date	Station	<u>Nos. of Fish Taken</u>		Comments
		C. bairdi	C. girardi	
8-27-77	4	55	18	
8-28-77	4	14	6	

APPENDIX B

SAMPLE SIZES USED IN MANN-WHITNEY OR KRUSKAL-WALLIS TESTS

(b = Cottus bairdi, g = Cottus girardi, m = male, f = female, i = immature)

Date	Station	mb	fb	ib	mg	fg	ig
2-10-77	3	4	3	3	0	0	2
2-10-77	4	6	3	8	0	0	4
2-10-77	5	2	0	7	0	0	0
3-5-77	1	0	0	3	0	0	0
3-5-77	2	0	0	0	0	0	7
3-5-77	3	2	5	4	0	0	0
3-5-77	5	0	2	1	0	0	0
3-19-77	3	0	0	9	0	0	8
3-19-77	4	11	0	4	0	0	3
4-16-77	4	6	2	14	0	0	8
4-16-77	5	2	0	6	0	0	5
5-11-77	1	0	0	8	2	2	8
5-11-77	2	0	0	0	2	0	5
5-11-77	4	3	5	7	2	1	6
6-20-76	5	3	0	8	0	2	4
6-25-77	4	2	1	7	0	1	5
6-25-77	5	0	1	10	2	1	2
7-25-76	4	0	3	4	0	0	4
7-25-76	5	1	3	3	0	0	0
8-27-77	4	3	3	19	3	5	4
8-28-77	4	0	0	11	0	0	5
11-1-76	4	2	1	13	1	0	4

LITERATURE CITED

- Addair, J. 1945. The fishes of the Kanawha River system in West Virginia and some factors which influence their distribution. Ph.D. Dissertation. Ohio State Univ. 225 p. (Seen in abstract only. Abstr. Doct. Diss. Ohio State Univ. 46: 9-17).
- Anderson, E.E., L.L. Smith, Jr. 1971. A synoptic study of food habits of 30 fish species from western Lake Superior. Minn. Agric. Exp. Stn., Tech. Bull. 279. 199 p.
- Anderson, R.V. 1975. Selective feeding of the sculpin, Cottus bairdi Girard, in Illinois. Trans. Ill. State Acad. Sci. 68(2): 118-121.
- Andreasson, S. 1968. Hybridisering mellan stensimpa och bergsimpa. (Hybridism between Cottus gobio L. and Cottus poecilopus Heckel.) (English summary). Fauna Flora (Stockh.) 63: 242-251.
- Andreasson, S. 1969a. Interrelations between Cottus poecilopus Heckel and C. gobio L. (Pisces) in a regulated north Swedish river. Oikos 20(2): 540-546.
- Andreasson, S. 1969b. Locomotory activity patterns of Cottus poecilopus Heckel and C. gobio L. (Pisces). Oikos 20(1): 78-94.
- Andreasson, S. 1972a. Distribution of Cottus poecilopus Heckel and C. gobio L. (Pisces) in Scandinavia. Zool. Scr. 1: 69-78.
- Andreasson, S. 1972b. Dag-och nattaktiva simpor. (Day and night activity of sculpins.) (English summary). Fauna Flora (Stockh.) 67: 229-232.
- Andreasson, S. 1973. Seasonal changes in diel activity of Cottus poecilopus and C. gobio (Pisces) at the Arctic Circle. Oikos 24(1): 16-23.
- Armstrong, J.G., and J.D. Williams. 1971. Cave and spring fishes of the southern bend of the Tennessee River. Tenn. Acad. Sci. 46(3): 107-115.
- Bailey, J.E. 1952. Life history and ecology of the sculpin Cottus bairdi punctulatus in southwestern Montana. Copeia (4): 243-255.

- Bailey, R. M., and C. E. Bond. 1963. Four new species of fresh water sculpins, genus Cottus, from western North America. Occas. Pap. Mus. Zool. Univ. Mich. 634: 1-27.
- Bailey, R. M., and M. F. Dimick. 1949. Cottus hubbsi, a new cottid fish from the Columbia River system in Washington and Idaho. Occas. Pap. Mus. Zool. Univ. Mich. 513: 1-18.
- Beaumont, P. 1975. Hydrology. Pages 1-38 in B. A. Whitton ed. Studies in ecology. Volume 2. River ecology. Univ. Calif. Press, Berkeley.
- Birch, L. C., and P. R. Ehrlich. 1967. Evolutionary history and population biology. Nature (Lond.) 214: 349-352.
- Blair, W. F., A. P. Blair, P. Brodkorb, F. R. Cagle, and G. A. Moore. 1957. Vertebrates of the United States. McGraw-Hill Book Co., New York. 819 p.
- Blankenship, S., and V. H. Resh. 1971. An unusual record of feeding in Cottus carolinae. Trans. Ky. Acad. Sci. 32: 10-11.
- Bond, C. E. 1963. Distribution and ecology of freshwater sculpins, genus Cottus, in Oregon. Ph.D. Dissertation. Univ. Mich. 198 p. (Seen in abstract only. Diss. Abstr. Int. B. Sci. Eng. 24(12): 5619).
- Borror, D. J., and D. M. DeLong. 1971. An introduction to the study of insects, 3rd ed. Holt, Rinehart, and Winston, New York. 812 p.
- Burton, G. W., and E. P. Odum. 1945. The distribution of stream fish in the vicinity of Mountain Lake, Virginia. Ecology 26(2): 182-194.
- Cady, R. C. 1936. Groundwater resources of the Shenandoah Valley, Virginia. Bull. Va. Geol. Surv. 45. 137 p.
- Cihar, J. 1969. Taxonomic and ecological notes on Cottus gobio Linnaeus, 1758, and Cottus poecilopus Heckel, 1836 (Osteichthyes: Cottidae). Vestn. Cesk. Spol. Zool. 33: 102-110.
- Coffman, W. P., K. W. Cummins, and J. C. Wuycheck. 1971. Energy flow in a woodland stream ecosystem: I. Tissue support trophic structure of the autumnal community. Arch. Hydrobiol. 68(2): 232-276.
- Colwell, R. K., and D. J. Futuyama. 1971. On the measurement of niche breadth and overlap. Ecology 52(4): 567-576.

- Craddock, J. E. 1965. Some aspects of the life history of the banded sculpin Cottus carolinae carolinae in Doe Run, Meade County, Kentucky. Ph.D. Dissertation. Univ. of Louisville. 175 p.
- Craig, P. C., and J. Wells. 1976. Life history notes for a population of slimy sculpin (Cottus cognatus) in an Alaskan arctic stream. J. Fish Res. Board Can. 33: 1639-1642.
- Crawford, D. R. 1927. Extension of the range of Cottus aleuticus. Copeia 160: 177-178.
- Cummins, K. W. 1964. A review of stream ecology with special emphasis on organism-substrate relationships. Pages 2-51 in K. W. Cummins, C. A. Tryon, Jr., and R. T. Hartman, eds. Organism-substrate relationships in streams. Pymatung Lab. Ecol., Spec. Pub. 4.
- Daiber, F. C. 1956. A comparative analysis of the winter feeding habits of two benthic stream fishes. Copeia (3): 141-151.
- Darwin, C. 1886. On the origin of species by means of natural selection, or the preservation of favored races in the struggle for life. D. Appleton and Co., New York. 458 p.
- Dineen, C. F. 1951. A comparative study of the food habits of Cottus bairdii and associated species of Salmonidae. Am. Midl. Nat. 46(3): 640-645.
- Downhower, J. F., and L. Brown. 1977. A sampling technique for benthic fish populations. Copeia (2): 403-406.
- Ebert, V. W., and R. C. Summerfelt. 1969. Contributions to the life history of the Piute sculpin, Cottus beldingi Eigenmann and Eigenmann, in Lake Tahoe. Calif. Fish Game 55(2): 100-120
- Eddy, S. 1969. How to know the freshwater fishes, 2nd ed. Wm. C. Brown Co., Dubuque. 286 p.
- Edmunds, G. F., Jr., S. L. Jensen, and L. Berner. 1976. The mayflies of North and Central America. Univ. Minn. Press, Minneapolis. 330 p.
- Emery, A. R. 1973. Preliminary comparisons of day and night habits of freshwater fish in Ontario Lakes. J. Fish Res. Board Can. 30(6): 761-774.
- Fish, M. P. 1932. Contributions to the early life histories of sixty-two species of fishes from Lake Erie and its tributary waters. U.S. Fish Wildl. Serv. Fish. Bull. 47(10): 294-371.

- Franz, R., and D. S. Lee. 1976. A relict population of the mottled sculpin, Cottus bairdi, from the Maryland coastal plain. Chesapeake Sci. 17(4): 301-302.
- Frison, T. H. 1935. The stoneflies, or Plecoptera, of Illinois. Ill. Nat. Hist. Surv. Bull. 20(4): 281-471.
- Gause, G. F. 1934. The struggle for existence. Williams and Wilkins, Baltimore. 163 p.
- Gibbons, J. R. H., and J. H. Gee. 1972. Ecological segregation between longnose and blacknose dace (genus Rhinichthys) in the Mink River, Manitoba. J. Fish. Res. Board Can. 29(9): 1245-1252.
- Greeley, J. R. 1932. The spawning habits of brook, brown and rainbow trout, and the problem of egg predators. Trans. Am. Fish. Soc. 62: 239-248.
- Hallam, J. C. 1959. Habitat and associated fauna of four species of fish in Ontario streams. J. Fish. Res. Board Can. 16(2): 147-173.
- Hann, H. W. 1927. The history of the germ cells of Cottus bairdii Girard. J. Morphol. Physiol. 43(2): 427-497.
- Hardin, G. 1960. The competitive exclusion principle. Science (Wash., D.C.) 131(29): 1292-1297.
- Harper, J. L., J. N. Clatworthy, J. H. McNaughton, and G. R. Sagan. 1961. The evolution and ecology of closely related species living in the same area. Evolution 15(2): 209-227.
- Harris, W. B. 1972. High silica resources of Clarke, Frederick, Page, Rockingham, Shenandoah, and Warren counties, Virginia. Va. Div. Mineral Resources, Va. Mineral Resource Rep. 11. 42 p.
- Hocutt, C. H., P. S. Hambrick, and M. T. Masnik. 1973. Rotenone methods in a large river system. Arch. Hydrobiol. 72(2): 245-252.
- Horn, H. S. 1966. Measurement of "overlap" in comparative ecological studies. Am. Nat. 100(914): 419-424.
- Hubbs, C. L. 1920. Further notes on the cottid fishes of the Great Lakes. Copeia 77: 1-3.
- Hubbs, C. L., and K. F. Lagler. 1958. Fishes of the Great Lakes region, 2nd ed. Univ. Mich. Press, Ann Arbor. 213 p.
- Hurlbert, S. H. 1978. The measurement of niche overlap and some relatives. Ecology 59(1): 67-77.

- Hynes, H. B. N. 1950. The food of fresh-water sticklebacks (Gasterosteus aculeatus and Pygosteus pungitius), with a review of methods used in studies of the food of fishes. J. Anim. Ecol. 19: 35-58.
- Hynes, H. B. N. 1970. The ecology of running waters. Univ. Toronto Press, Toronto. 555 p.
- Keast, A. 1977. Mechanisms minimizing intraspecific competition in vertebrates, with a quantitative study of the contrasting strategies of two centrarchid fishes, Ambloplites rupestris and Lepomis macrochirus. Evol. Biol. 10: 333-395.
- Kohn, A. J., and G. H. Orians. 1962. Ecological data in the classification of closely related species. Syst. Zool. 11(3): 2119-2127.
- Koster, W. J. 1937. The food of sculpins (Cottidae) in central New York. Trans. Am. Fish. Soc. 66: 374-382.
- Kovalak, W. P. 1978. Relationships between size of stream insects and current velocity. Can. J. Zool. 56(2): 178-186.
- Lee, D. S., A. Norden, C. R. Gilbert, and R. Franz. 1976. A list of the fresh water fishes of Maryland and Delaware. Chesapeake Sci. 17(3): 205-211.
- Loos, J. J., W. S. Woolcott, and N. R. Foster. 1972. An ecologist's guide to the minnows of the freshwater drainage systems of the Chesapeake Bay area. Bull. Assoc. Southeast Biol. 19(3): 126-138.
- Ludwig, G. M., and E. L. Lange. 1975. The relationship of length, age, and age-length interaction to the fecundity of the northern mottled sculpin, Cottus b. bairdi. Trans. Am. Fish. Soc. 104(1): 64-67.
- Ludwig, G. M., and C. R. Norden. 1969. Age, growth and reproduction of the northern mottled sculpin (Cottus bairdi bairdi) in Mt. Vernon Creek, Wisconsin. Milw. Public Mus. Occas. Pap. Nat. Hist. (2): 1-67.
- Manion, P. J. 1977. Downstream movement of fish in a tributary of Lake Superior. Prog. Fish-Cult. 39(1): 14-16.
- Mason, J. C., and S. Machidori. 1976. Populations of sympatric sculpins, Cottus aleuticus and Cottus asper, in four adjacent salmon-producing coastal streams on Vancouver Island, B.C. U.S. Nat. Mar. Fish. Serv. Fish. Bull. 74(1): 131-141.

- McCleave, J. D. 1964. Movement and population of the mottled sculpin (Cottus bairdi Girard) in a small Montana stream. *Copeia* (3): 506-513.
- McEachran, J. D., and C. O. Martin. 1977. Possible occurrence of character displacement in the sympatric skates Raja erinacea and R. ocellata (Pisces: Rajidae). *Env. Biol. Fishes* 2(2): 121-130.
- Mendelson, J. 1975. Feeding relationships among species of Notropis (Pisces: Cyprinidae) in a Wisconsin stream. *Ecol. Monogr.* 45(3): 199-230.
- Minckley, W. L. 1963. The ecology of a spring stream: Doe Run, Meade County, Kentucky. *Wildl. Monogr.* 11. 124 p.
- Minckley, W. L., J. E. Craddock, and L. A. Krumholz. 1963. Natural radioactivity in the food web of the banded sculpin Cottus carolinae (Gill). Pages 229-236 in E. V. Schultz and A. W. Klement, Jr., eds. *Radioecology*. Reinhold Pub. Co., New York.
- Moyle, P. B. 1976. *Inland fishes of California*. Univ. Calif. Press, Berkeley. 405 p.
- Needham, J. C., and M. J. Westfall, Jr. 1955. *A manual of the dragonflies of North America (Anisoptera)*. Univ. Calif. Press, Berkeley. 615 p.
- Nie, N. H., C. H. Hull, J. G. Jenkins, K. Steinbrenner, and D. H. Bent. 1975. *SPSS: Statistical package for the social sciences*, 2nd ed. McGraw-Hill Book Co., New York. 675 p.
- Northcote, T. G. 1954. Observations on the comparative ecology of two species of fish, Cottus asper and Cottus rhotheus, in British Columbia. *Copeia* (1): 25-28.
- Nursall, J. R. 1974. Character displacement and fish behavior, especially in coral reef communities. *Am. Zool.* 14: 1099-1118.
- Pasch, R. W., and J. H. Lyford, Jr. 1972. The food habits of two species of Cottus occupying the same habitat. *Trans. Am. Fish. Soc.* 101(2): 377-381.
- Patten, B. G. 1971. Spawning and fecundity of seven species of north-west American Cottus. *Am. Midl. Nat.* 85(2): 493-506.
- Pearse, A. S. 1918. The food of the shore fishes of certain Wisconsin lakes. *Bull. U.S. Bur. Fish.* 35(1915-1916): 247-292.

- Pennak, R. W. 1978. Fresh-water invertebrates of the United States, 2nd ed. John Wiley & Sons, New York. 803 p.
- Reighard, J. 1915. An ecological reconnaissance of the fishes of Douglas Lake, Cheboygan County, Michigan, in mid-summer. Bull. U.S. Bur. Fish. 33(814): 215-249.
- Robins, C. R. 1954. A taxonomic revision of the Cottus bairdi and Cottus carolinae species groups in eastern North America (Pisces, Cottidae). Ph.D. Thesis, Cornell Univ. 230 p.
- Robins, C. R. 1961. Two new cottid fishes from the fresh waters of eastern United States. Copeia (3): 305-315.
- Robins, C. R., and R. R. Miller. 1957. Classification, variation, and distribution of the sculpins, genus Cottus, inhabiting Pacific slope waters in California and southern Oregon, with a key to the species. Calif. Fish Game. 43(3): 213-233.
- Ross, S. T. 1977. Patterns of resource partitioning in searobins (Pisces: Triglidae). Copeia (3): 561-572.
- Sale, P. F. 1974. Overlap in resource use and interspecific competition. Oecologia (Berl.) 17: 245-256.
- Savage, T. 1962. Cottus girardi Robins, a synonym of Cottus bairdi Girard. Copeia (2): 848-850.
- Savage, T. 1963. Reproductive behavior of the mottled sculpin, Cottus bairdi Girard. Copeia (2): 317-325.
- Schoener, T. W. 1968. The Anolis lizards of Bimini: resource partitioning in a complex fauna. Ecology 49(4): 704-726.
- Schoener, T. W. 1974. Resource partitioning in ecological communities. Science (Wash., D.C.) 185: 27-39.
- Schultz, L. P. 1930. Notes on the species of Cottus in western Washington. Copeia (1): 14-15.
- Scott, W. B., and E. J. Crossman. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. 184. 966 p.
- Seigel, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York. 312 p.
- Simon, J. R., and R. C. Brown. 1943. Observations on the spawning of the sculpin, Cottus semiscaber. Copeia (1): 41-42.

- Small, J. W., Jr. 1975. Energy dynamics of benthic fishes in a small Kentucky stream. *Ecology* 56(4): 827-840.
- Smith, B. G. 1922. Notes on the nesting habits of Cottus. *Pap. Mich. Acad. Sci. Arts Lett.* 2: 222-224.
- Sokal, R. R., and F. J. Rohlf. 1969. *Biometry: The principles and practice of statistics in biological research.* W. H. Freeman and Co., San Francisco. 776 p.
- Starmach, J. 1962. Koppen in den Karpathenflüssen. I. Vermehrung, embryonale und larvale Entwicklung bei Cottus poecilopus Heckel. (Bullheads of the Carpathian rivers. I. Reproduction embryonic and larval development of Cottus poecilopus Heckel.) (Polish summary). *Acta Hydrobiol.* 4(3-4): 321-343. (Seen in abstract only. *Biol. Abstr.* 46(3): 926).
- Starmach, J. 1970. The number of erythrocytes in the blood of Cottus poecilopus Heckel and Cottus gobio L. *Acta Biol. Cracov. Ser. Zool.* 13(2): 243-249. (Seen in abstract only. *Biol. Abstr.* 53(8): 4093.)
- Starmach, J. 1971. Oxygen consumption and respiratory surface of gills in Cottus poecilopus Heckel and Cottus gobio L. *Acta Biol. Cracov. Ser. Zool.* 14(1): 9-15. (Seen in abstract only. *Biol. Abstr.* 54(1): 517.)
- Starmach, J. 1972. Charakterystyka glowaczy: Cottus poecilopus Heckel i Cottus gobio L. (Characteristic of Cottus poecilopus Heckel and Cottus gobio L.) (English summary). *Acta Hydrobiol.* 14(1): 67-102. (Seen in abstract only. *Biol. Abstr.* 54(10): 5183.)
- Straskraba, M., J. Chiar, S. Frank, and V. Hruska. 1966. Contribution to the problem of food competition among the sculpin, minnow and brown trout. *J. Anim. Ecol.* 35: 303-311.
- Strauss, R. E. 1977. Morphometric and electrophoretic analysis of the systematic status of Cottus girardi Robins (Pisces: Cottidae). Master's Thesis, Penn. State Univ. 125 p.
- Thorup, J. 1964. Substrate type and its value as a basis for the delimitation of bottom fauna communities in running waters. Pages 59-74 in K. W. Cummins, C. A. Tryon, Jr., and R. T. Hartman, eds. *Organism-substrate relationships in streams.* Pymatung Lab, Ecol., Pub. 4.
- Turner, C. L. 1922. Notes on the food habits of young of Cottus ictalops (millers thumb). *Ohio J. Sci.* 95-96.

Usinger, R. L., ed. 1956. Aquatic insects of California. Univ. Calif. Press, Berkeley. 508 p.

Walker, W. H. 1975. Trophic relationships of the mottled sculpin, Cottus bairdi in a woodland stream, Linesville Creek, Crawford County, Pennsylvania. Ph.D. Dissertation, Univ. Pittsburgh. 378 p. (Seen in abstract only. Diss. Abstr. Int. B. Sci. Eng. 36: 3186-B.)

Ward, H. B., and G. C. Whipple. 1959. Fresh-water biology, 2nd ed. John Wiley & Sons, New York. 1248 p.

Werner, E. E. 1977. Species packing and niche complementarity in three sunfishes. Am. Nat. 111(979): 553-578.

Werner, E. E., and D. J. Hall. 1976. Niche shifts in sunfishes: experimental evidence and significance. Science (Wash., D. C.) 191: 404-406.

Werner, E. E., D. J. Hall, D. R. Laughlin, D. J. Wagner, L. A. Wilsmann, and F. C. Funk. 1977. Habitat partitioning in a freshwater fish community. J. Fish Res. Board Can. 34(3): 360-370.

Wiggins, G. B. 1977. Larvae of the North American caddisfly genera (Trichoptera). Univ. Toronto Press, Toronto. 401 p.

Williams, J. D., and C. R. Robins. 1970. Variation in populations of the fish Cottus carolinae in the Alabama River system with a description of a new subspecies from below the fall line. Am. Midl. Nat. 83(2): 368-381.

Zarbock, W. M. 1952. Life history of the Utah sculpin, Cottus bairdi semiscaber (Cope), in Logan River, Utah. Trans. Am. Fish. Soc. 81: 249-259.

Zaret, T. M., and A. S. Rand. 1971. Competition in tropical stream fishes: support for the competitive exclusion principle. Ecology 52: 336-342.

VITA

Richard Edmond Matheson, Jr.

Born in Knoxville, Tennessee, March 24, 1952. Graduated from Alcoa High School, Alcoa, Tennessee in 1970. Attended University of Tennessee 1970 through 1973 and received B.S. from the College of William and Mary in 1975. Entered M.A. program in the Department of Biology at the College of William and Mary in 1975.

In September 1978, the author entered graduate school as a Ph.D. student at Texas A&M University.