

AN ABSTRACT OF THE THESIS OF

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Title: Patterns of Interactive Segregation in Three Species of
Sculpins (Cottus) in Western Oregon.

Abstract approved:

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James D. Hall

Species interactions and their effect on the use of habitat by benthic fishes were examined in a guild composed of Cottus perplexus, C. rhotheus, and C. beldingi in the Marys River above Philomath, Oregon, and in a constant environment provided by an artificial stream.

In the Marys River system, the pattern of longitudinal succession in this guild was one of species additions downstream rather than sequential longitudinal replacement. Cottus perplexus occurred throughout the river system, C. rhotheus was found only in the middle and lower reaches, and C. beldingi was restricted to the lower reaches within the study area. Longitudinal distributions appeared to be most strongly related to substrate characteristics in riffles. Cottus perplexus occurred on all substrates, C. rhotheus was found only where rock was present, and C. beldingi was captured only in riffles dominated by loose, cobble-sized rock with many interstitial spaces.

Local use of habitat was strongly related to the breadth of environmental tolerance of each species and the presence or absence of other Cottus species. The species broadly overlapped in their

use of different substrates, depths, and distances from shore, but segregated in an orderly manner with respect to current velocity. Where it existed alone, C. perplexus utilized both pools and riffles and was found in greatest densities near cover. Where it coexisted with C. rhotheus, C. perplexus was primarily confined to pools and declined significantly in abundance. The degree to which C. perplexus was excluded from riffles varied in relation to seasons and the size composition of the C. rhotheus population. In areas where there were low densities of large C. rhotheus, the exclusion of C. perplexus was not as pronounced as in areas where there were many large C. rhotheus, and was apparently due mainly to competition. In these areas overlap between the species was also greater in spring, the time of peak food abundance, than in summer or winter. In areas where there were greater numbers of large C. rhotheus, the exclusion of C. perplexus from riffles was more pronounced and did not vary seasonally. In these areas predation was apparently the most important mechanism causing the interactive segregation. Cottus rhotheus was generally confined to riffles, although some large individuals did wander into pools during times of food scarcity. Cottus beldingi was exclusively found in riffles and had a greater maximum current velocity tolerance than C. rhotheus. In summer, all riffle areas in the Marys River flowed slowly enough for C. rhotheus, and C. beldingi apparently was forced, by predation and competition exerted by C. rhotheus, to burrow into the substrate. In winter and spring, C. rhotheus was excluded from areas of some riffles by the faster currents. In these areas C.

beldingi had a refuge from competition and predation and was found atop the substrate to a greater degree.

Experiments with the three species in the artificial stream supported the field data and suggested that the competition contributing to the habitat shifts was interference competition for space. Cottus perplexus selected riffle areas when alone, but was displaced partially to pools by C. beldingi through interference competition. The addition of C. rhotheus caused C. perplexus to be more rigidly confined to pools, but C. beldingi was able to coexist in riffles with C. rhotheus apparently by utilizing the interstitial spaces in the substrate.

Comparison of these results with those of other studies suggests that segregation in stream fishes should be more commonly based on habitat than on food or time. A model was constructed that could be used to predict patterns of habitat utilization in other guilds of benthic fishes. Species interactions were also suggested as having a major influence on the evolutionary patterns of Cottus in western North America. Large, dominant species will obtain their preferred habitat throughout their geographical range. They will therefore not need to adapt to a wide range of conditions and thus may exhibit low morphological variability. Contrastingly, less dominant species may be forced into many different habitats, depending on which dominant species are also present, and may thus exhibit greater morphological variability.

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Patterns of Interactive Segregation in Three Species
of Sculpins (Cottus) in Western Oregon

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PATTERNS OF INTERACTIVE SEGREGATION IN THREE SPECIES
OF SCULPINS (COTTUS) IN WESTERN OREGON

INTRODUCTION

It seems that it is perhaps time that we made a conscious effort to separate ecology from fishery biology, and that the ecologists should forget that fishes can be eaten and angled for and start to try to find out more about them as animals. ... This then is a plea for a more general approach by many students of fishes to the problems of fish ecology.

H. B. N. Hynes (1970)

The analysis of niche interrelationships that affect the distribution and abundance of species is central to ecology. There is little question that species interactions strongly influence community structure, both by affecting patterns over short ecological time spans (e.g., see MacArthur 1972; Schoener 1974; Cody and Diamond 1975; Pianka 1976) and by influencing the long term evolutionary pathways taken by coexisting organisms (Bock 1972; Boucot 1975, 1978). These interactions can occur in different environmental contexts and between species with different evolutionary strategies; their effects can be expected to be influenced by both short- and long-term trends in environmental variability and by intraspecific competition (Wiens 1977; Keast 1977). To assess these interactions and the resulting patterns of community structure therefore requires careful consideration of the evolutionary, biogeographical, and natural histories of the species and of the magnitude and time resolution of environmental

fluctuations.

Many of these concepts have been considered both theoretically and empirically in the ecological literature. Most work, however, has been oriented toward homeotherms and other terrestrial organisms; the patterns of community structure and organization in stream fishes remain largely unexplored. Keast (1977) and Werner (1977) have discussed aspects of the life history patterns of freshwater fishes and the peculiarities of the freshwater environment that make many of the concepts derived from terrestrial studies not directly applicable to fishes. Of the studies that have examined species interactions in freshwater fishes and the resulting community structure (Lagler 1944; Hartley 1948; Nilsson 1967, 1978; Lowe-McConnell 1975; Keast 1977; Werner 1977; Werner and Hall 1976, 1977; Werner et al. 1977; Kerr and Ryder 1977; Ryder and Kerr 1978), most have dealt with lentic species. In streams, the patterns of environmental variability and the evolutionary strategies of fishes may be quite different from those in lakes. The documentation of specific patterns in stream fishes coupled with the development of a theoretical framework thus assumes critical importance, both to increase understanding of stream environments and as a valuable comparison of terrestrial and lentic studies.

MacArthur (1972) noted that ecological investigation of organisms and environments not previously well-studied should begin where intuition indicates that the patterns in question should be most apparent. After fundamental mechanisms are resolved and

integrated into a theoretical framework, the investigation of more complex problems can progress. With regard to species interactions and the resulting community structure, ecological intuition indicates that the patterns should be clearest in guilds, groups of coexisting species that utilize a similar resource base (Root 1967). Further, if the guild exists in relative isolation and contains a small number of species, interactions within the guild can be readily analyzed because they will be free from diffuse competition (MacArthur 1972; Cody 1974), selective predation on members of the guild by species not in the guild (Paine 1966; Nilsson 1978), and other complex, confusing factors. In the northwestern United States, the sculpins (genus Cottus) appear to be excellent subjects for initial investigations of the patterns of community organization in stream fishes. They dominate the fish fauna in many lotic environments throughout the region; in numerous streams small groups of sculpins form guilds that exist in relative isolation from the few other fish species present. Thirteen species of sculpins are found in Oregon alone, but the distribution patterns of these species are remarkably patchy (Bond 1963). As a result, Oregon rivers form an array where the species exist under a variety of environmental conditions and in different combinations of co-occurrence. The geologic structure of the region is also relatively recent, enabling the biogeographical histories of the species to be traced with more certainty than would be possible with an older fauna.

The careful documentation of specific patterns of species interactions and the resulting structure in even a small, isolated

guild requires a considerable amount of intensive study; in this thesis only the patterns in a single sculpin guild could be specifically delineated. This study will therefore deal with the documentation of the patterns in three species that widely coexist in the Willamette drainage basin in Oregon, Cottus perplexus, C. rhotheus, and C. beldingi. These results and information from the literature will then be utilized to investigate general ecological and evolutionary patterns in benthic stream fishes in relation to species interactions.

The objectives of this thesis are therefore:

- 1) To document the patterns of species interactions and resulting structure in a guild composed of Cottus perplexus, C. rhotheus, and C. beldingi.
- 2) To assess the relative importance of competition, predation, and environmental variability with regard to their influence on the structure of stream fish communities.
- 3) To discuss the effects of species interactions on the evolutionary and biogeographical history of Cottus in western North America.

CONCEPTUAL FOUNDATION

Natural History of Cottus

Sculpins of the genus Cottus are freshwater representatives of the predominantly marine family Cottidae. They are circumpolar in distribution and occupy benthic habitats in both lotic and lentic environments. Cottus, particularly in western North America, contains an extensive array of morphological types; their systematics are as yet only partially understood (Bailey and Dimick 1949; Robins and Miller 1957; McAllister and Lindsey 1961; Bailey and Bond 1963). Convergent and divergent evolution, as well as the possibility of several independent entries into fresh water by different marine ancestors, have contributed to these taxonomic difficulties.

In addition to their morphological likeness, species of Cottus also exhibit a great deal of similarity in food habits, diel activity patterns, and reproductive behavior. The major ecological differences among species appear to be in habitat selection and secondarily in those factors related to habitat and to the differences in size attained by each species.

The diets of the Cottus species that have been examined all show marked similarity. Major food items are aquatic insect larvae, although fish are occasionally taken, especially by the larger species (Koster 1937; Dineen 1951; Miller 1951; Bailey 1952; Zarbock 1952; Northcote 1954; Daiber 1956; Dietsch 1959; Patten 1962; Bond 1963; Straskraba et al. 1966; McLarney 1967; Millikan 1968; Mann and

Orr 1969; Ebert and Summerfelt 1969; Andreasson 1971; Blankenship and Resh 1971; Antonelli et al. 1972; Clary 1972; Jones 1972; Pasch and Lyford 1972; Novak and Estes 1974; Ringstad 1974; Petrosky and Waters 1975; Small 1975; Li and Moyle 1976; Mason and Machidori 1976; Moyle 1977; Daniels and Moyle 1978). Differences in diet that have been observed reflect differences in habitat or mouth gape. Feeding therefore appears to be opportunistic rather than influenced by any active selection of prey. Diel activity patterns in feeding also appear to be similar in all species of Cottus. Although sculpins are more likely to abandon cover at night (Bond 1963; Baker and Cordone 1969), feeding occurs continuously throughout the day and night with an activity peak near dawn (Ringstad 1974; Li and Moyle 1976).

Reproductive behavior is also relatively uniform within the genus. Most species mature after their second year, spawn in spring, and have similar nesting behavior (e.g., see Smith 1922; Simon and Brown 1943; Bailey 1952; Morris 1955; Bond 1963; Savage 1963; McLarney 1968; Patten 1971; Jones 1972). Patten (1971) stated that the high intraspecific variability in fecundity in inland species makes comparisons among species meaningless. Spawning migrations by several coastal species have been observed (Shapovalov and Taft 1954; Hunter 1959; Taylor 1966; Kresja 1967), but inland species tend to breed in the same habitats used during the remainder of the year. Observed spawning movements in these species (e.g., Thomas 1973) appear to be local in nature.

Most larval freshwater sculpins are quite morphologically advanced at hatching (Sheldon 1968a; Hogue et al. 1976; Finger et al., in prep.) and immediately assume a benthic existence. Habitats used by larvae, however, often differ from those utilized by the adults of the same species (Bailey 1952; Bond 1963). In at least some lotic species, larvae appear to drift downstream, perhaps as a means of dispersal (Sheldon 1968a).

The three species intensively studied in this thesis, Cottus perplexus, C. rhotheus, and C. beldingi, appear to be typical of the genus. All have similar patterns of feeding, diel activity, and reproduction; they differ, however, in size and in habitat preference.

The reticulate sculpin, Cottus perplexus, is distributed along the west coast of North America from the Rogue River north into Washington and is widespread inland in western Oregon (Bond 1963). Like most species of Cottus, the reticulate sculpin feeds primarily on aquatic insect larvae (Bond 1963), matures after its second year, and spawns in spring (Patten 1971). Although riffles are preferred for breeding, C. perplexus is capable of successfully spawning in the absence of current.

Cottus perplexus grows somewhat more slowly and has a smaller maximum size than most freshwater sculpins (Bond 1963). Maximum age appears to be 6 years, and although individuals over 100 mm in standard length have been collected from eutrophic ponds, stream dwelling reticulate sculpins rarely exceed 75 mm in length.

The reticulate sculpin inhabits both lotic and lentic environments. In streams, C. perplexus appears to prefer rock rubble substrates in riffles when it occurs alone, but is more abundant in pools and silty stream margins when it coexists with other sculpin species (Bond 1963). Although no evidence of this shift was found by Pasch and Lyford (1972), their data indicate that they confused C. perplexus with the riffle dwelling C. beldingi. In addition to its acceptance of a wide range of current velocities and substrates, Bond (1963) found that C. perplexus was more resistant to low oxygen levels and rapid temperature changes than either C. rhotheus or C. beldingi. Although Phillips and Claire (1966) found that under laboratory conditions the reticulate sculpin was capable of burrowing into gravel, Bond (1963) noted that this species is more likely to be found exposed during daylight hours than are other sculpins. This is particularly true of the larvae, which inhabit silt substrates along pool margins.

The torrent sculpin, Cottus rhotheus, is widespread in the Columbia River drainage in Oregon, Washington, Idaho, and British Columbia. Although C. rhotheus also occurs in the Puget Sound drainage and numerous coastal rivers in Washington, its coastal distribution in Oregon is limited to a few rivers on the north coast which it has entered from the Columbia (McAllister and Lindsey 1961; Bond 1963). Cottus rhotheus grows more rapidly and reaches a larger maximum size than most freshwater sculpins. Bond (1963) noted that the torrent sculpin can live at least 6 years; McAllister and

Lindsey (1961) gave the maximum total length as approximately 155 mm. Like most members of the genus, C. rhotheus feeds primarily on aquatic insect larvae, but because of its larger size, the torrent sculpin does consume proportionately more fish than many species (Northcote 1954; Patten 1962; Bond 1963; Pasch and Lyford 1972). Also typical for the genus, the torrent sculpin spawns in spring, and although it may also be typical in maturing after its second year, in some populations C. rhotheus may not spawn until its third or fourth year (Northcote 1954; Bond 1963).

Although C. rhotheus is occasionally found in lakes, it is primarily an inhabitant of large streams (Northcote 1954; Bond 1963). In rivers it prefers rock rubble substrates in riffles and usually retreats under the first layer of stones during daylight hours. At night the torrent sculpin tends to abandon cover and may forage in pools and along shallow stream margins (Bond 1963). As is the case with C. perplexus, juvenile torrent sculpins are more likely to be found exposed than are the adults. Although Bond (1963) found that the maximum temperature tolerance of C. rhotheus was similar to that of C. perplexus and C. beldingi, the torrent sculpin was more sensitive to rapid changes in temperature than either of these species.

The Piute sculpin, Cottus beldingi, is widespread in the Columbia River drainage in Oregon and Washington and also inhabits the Lahontan, Bonneville, and upper Colorado River systems (Bond 1963; Moyle 1976). Like most species of Cottus, the Piute sculpin

is an opportunistic feeder, matures after its second year, and spawns in spring (Miller 1951; Dietsch 1959; Bond 1963; Ebert and Summerfelt 1969; Patten 1971; Jones 1972).

Cottus beldingi grows somewhat more slowly than most freshwater sculpins, although its growth rate exceeds that of C. perplexus at least during the first two years of life (Bond 1963). The maximum age appears to be 6 years. Individuals as large as 130 mm in total length have been collected from lakes, but stream dwelling Piute sculpins are generally somewhat smaller (Dietsch 1959; Jones 1972).

The Piute sculpin inhabits both lotic and lentic environments. In streams it is primarily found in the middle reaches of drainage basins and reaches maximum densities in riffles with rubble and gravel substrates (Bond 1963; Jones 1972; Gard and Flittner 1974). Cottus beldingi has greater burrowing ability than most sculpins; Bond (1963) noted that it may burrow down into gravel 30 cm or more during daylight hours and come up near the surface of the substrate at night. The larvae appear to occupy habitats similar to those used by the adults and are known to drift downstream for several weeks after hatching (Sheldon 1968a). Although Bond (1963) found that C. beldingi was more sensitive to low oxygen concentrations than either C. perplexus or C. rhotheus, the maximum temperature tolerances of these species were all similar. The Piute sculpin was, however, found to be more sensitive to rapid temperature changes than C. perplexus, but less sensitive than C. rhotheus.

Mechanisms Producing Community Structure

The majority of recent empirical studies investigating the mechanisms that produce community structure have determined the patterns of resource partitioning among closely related, coexisting species and inferred that these patterns were structured by interspecific competition. Reviews of these empirical findings indicate that orderly patterns of resource partitioning do exist in a wide variety of organisms (Schoener 1974; Pianka 1976); the integration of these observations with competition theory has generally been considered highly successful (e.g., see Hutchinson 1975; Diamond 1978). Interference or exploitation competition are, however, extremely difficult to document directly in the field. They require either the observation of agonistic behavior or evidence that a resource in common use by coexisting individuals is limiting. The presence of competition has therefore usually been inferred through the documentation of niche shifts, character displacement, and other indirect evidence (see reviews by Grant 1972; Cody 1973; Hespenheide 1973; Schoener 1974; Pianka 1976). As a result, the interaction of competition theory and empirical study has recently been questioned (Connell 1975; Peters 1976; Wiens 1977). The plausible portions of these arguments do not appear to question that interspecific competition does, in fact, occur, but rather attack the uncritical acceptance of the belief that competition always acts severely and continuously to produce organisms that are optimally suited to their environment and that it therefore is the

major mechanism producing community structure.

These objections have served to illustrate the need to also consider predation, intraspecific competition, and environmental variability as factors that may influence community structure. Hairston et al. (1960) and Menge and Sutherland (1976) have discussed conditions where either predation or interspecific competition could be expected to be the most important mechanism producing community structure. Macan (1974) evaluated the relative importance of these factors with specific regard to freshwater communities. Colwell and Fuentes (1975) have noted that niche shifts similar to those caused by interspecific competition may also result from predation. Alternatively, Connell (1975) stated that in some instances predation can hold prey species densities so low that competition never occurs. Keast (1977) has discussed the effects of intraspecific competition. He noted that although interspecific competition can act to restrict the range of resource utilization by a species, intraspecific competition can contrastingly act to expand this range and can also affect patterns among age classes of the species. In much ecological work, the magnitude and time resolution of environmental variability are not considered. Hutchinson (1957, 1961) has discussed the effects of temporal environmental variability on competitive relations in lacustrine systems. Fretwell (1972) and Wiens (1976, 1977) noted that the effects of a variable environment and the resulting periodic relaxations of competition can invalidate many theoretical treatments

of mechanisms producing community structure.

This evidence indicates that competition, predation, and environmental variability all have the potential for influencing community structure. Which factor does dominate in any particular instance depends on the organisms and environment in question. All of these mechanisms may be operating within the guild composed of the three sculpin species that are the focus of this study. No presupposition of their relative importance will therefore be made. The patterns of separation of species resulting from species interactions will be considered as interactive segregation (after Nilsson 1967, 1978) because they may be caused by any mechanism, and will be viewed in a context that also considers intraspecific interactions and environmental variability.

Guilds and Hierarchical Structure

This thesis will deal solely with the species interactions within a guild of benthic fishes. The question therefore arises as to the validity of studying these interactions in isolation from the other coexisting species that may also interact with members of the guild. Isolating a guild has obvious practical benefits, and when ecological systems are viewed with regard to their hierarchical structure, the validity of this isolation can be justified in many circumstances. The following development is largely a synthesis of portions of the general systems theory works of Simon (1965), Koestler (1967, 1978), and von Bertalanffy (1968).

Although one of the cliches of modern ecology is that all organisms are interconnected with all others, the knowledgeable naturalist recognizes that these connections are of greatly differing types and magnitudes. For example, the fish species in a river are individually connected to each species of benthic invertebrate, but these connections are quite different from those among the fishes themselves. Interactions among fishes may include agonistic behavior and associated interference competition, but such relations do not appear to occur commonly between stream fishes and benthic invertebrates. Similarly, although both fish-fish and fish-invertebrate interactions may include exploitation competition and predation, the different turnover rates and standing crop biomasses associated with these two groups result in interactions of different magnitudes.

Rather than deal with the impracticality of considering individual interactions among all pairs of coexisting species, the relations can be classified as to their type and magnitude and a system can be organized based on this classification. A system thus organized will generally have a hierarchical structure. Species with similar interactions, both with respect to type and magnitude, are grouped into guilds; these guilds form the subgroups of the next hierarchical level. The species of one guild do, of course, interact with the species of other guilds, but because these interactions are fundamentally different from those within the guild, they are not considered at the between species level, but rather at the between

guild level.

A portion of a hierarchical system based on the fauna of many of the streams of the Willamette River drainage in western Oregon is shown in Figure 1. The interactions among the benthic vertebrates, in this case three species of Cottus, are considered at the species level, while the relations between the benthic vertebrates and invertebrates are relegated to the next higher level and considered as interactions between guilds. Thus, such interactions as predation and competition among the benthic fishes can be considered individually in isolation. Conversely, such interactions as exploitation competition between sculpins and large stoneflies, which has been documented under laboratory conditions (Davis and Warren 1965), could be considered as exploitation competition between guilds, rather than separately as an array of competitive relations between each sculpin and stonefly species pair.

Such a system must, however, be constructed with consideration of the natural histories of the species and environment and the specific problem under investigation. For example, if selective predation on the members of a guild by species not in the guild were a major factor influencing guild structure (e.g., Paine 1966; Nilsson 1978), such a system would not be suitable for the investigation of mechanisms affecting guild structure. The problem formulation must therefore be guided by the investigator's tacit knowledge of the system (Polanyi 1966).

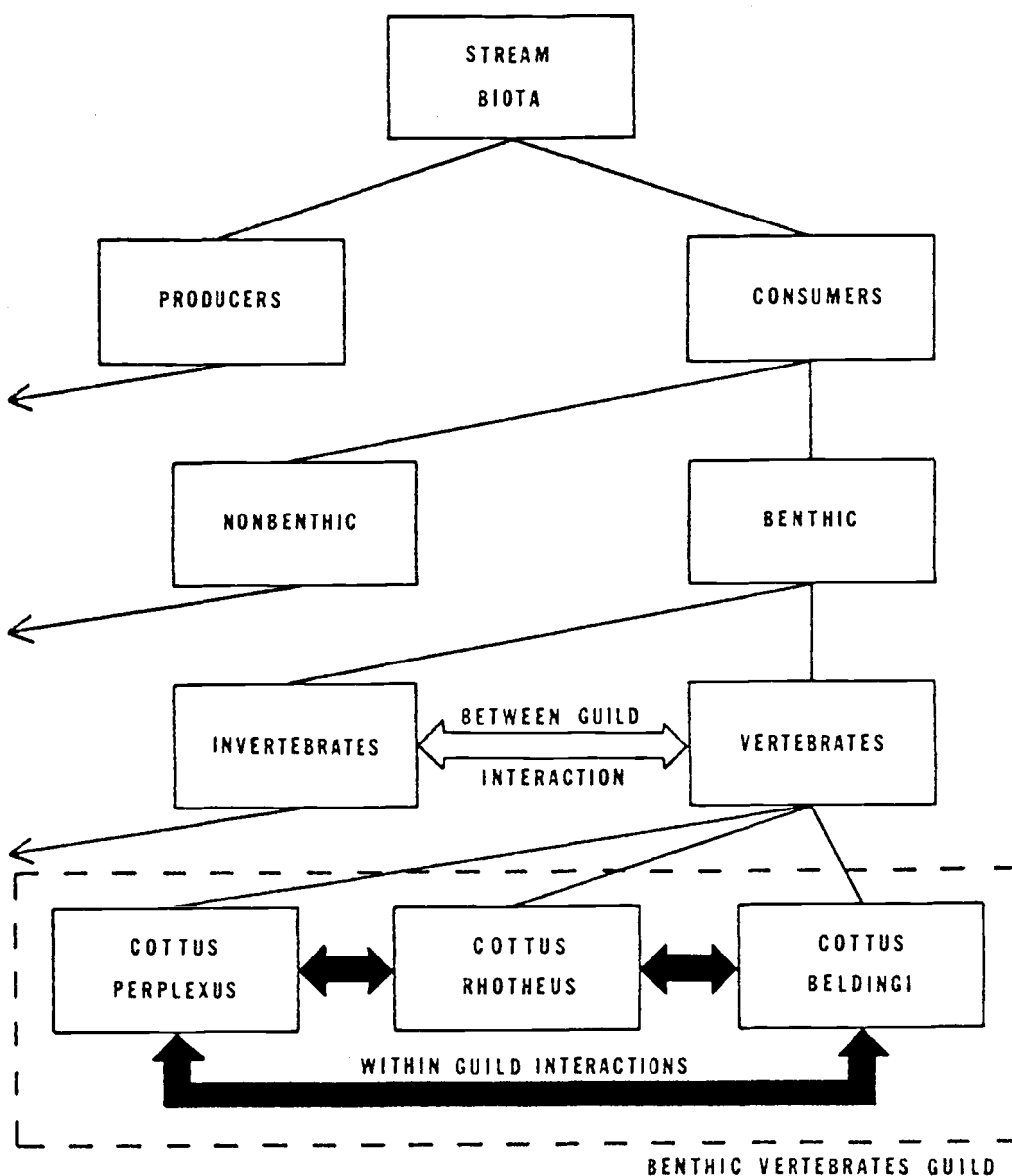


Figure 1. A portion of a hierarchically organized system based on the fauna of many of the streams of the Willamette River drainage in western Oregon. For clarity, only those portions of the system considered in this thesis are shown in detail.

In the case of the Coast Range streams of the Willamette River drainage in western Oregon, the construction and use of such a hierarchy is simplified by the depauperate nature of the fauna. Species of the genus Cottus, both in numbers and biomass, dominate the vertebrate fauna of the rivers (Bond 1963, 1973). If other vertebrates actually belong in the same guild (e.g., Rhinichthys and Dicamptodon), the effect of omitting them is negligible due to their relative scarcity. Also, there does not appear to be any predator that has the potential for selectively feeding on Cottus species and thus affecting guild structure. Salmo clarki is the only relatively common predator present and in most locations it appears to be too uncommon to affect sculpin abundance significantly. The hierarchy presented in Figure 1 was therefore considered appropriate to study the mechanisms affecting the structure of the guild of benthic vertebrates and represents a rationale for investigating the interactions within the guild in isolation.

Guild Structure in Stream Fishes

The number of environmental variables upon which coexisting species may segregate is potentially infinite. A large number of ecological factors may affect the species, and each factor may be expressed in an infinite number of ways. Pianka (1974) noted, however, that all possible variables can be considered as different expressions of three fundamental factors: food, time, and space.

In the case of the stream dwelling Cottus, the natural history literature reviewed above indicates that food and time are not divided to any great extent among the species. All lotic sculpins are opportunistic feeders, follow the same diel activity patterns, and breed at the same time of year. Space appears to be the most important potentially divisible variable upon which interactive segregation in sculpin guilds may be based. This study therefore focused on the differential use of space (i.e., habitat utilization) by the three coexisting species of Cottus.

Space can be considered on several levels of resolution. The use of these levels helps to avoid the confusion that arises from the nonspecific use of the terms allopatry and sympatry. For stream fishes, the following levels are convenient:

1) Geographical - separation by river system. For example, Burton and Odum (1945) noted that several contiguous river systems had relatively few species in common and attributed their lack of similarity to differences in the physical environment in each river. More recently, Page and Schemske (1978) noted that several species of pool dwelling Etheostoma are separated on this scale and suggested that competition is the primary cause.

2) Longitudinal - separation within a river system along its length. Hynes (1970) and Hawkes (1975) have recently reviewed much evidence for the longitudinal separation of stream fish species. In the case of Cottus, Bond (1963) noted that although C. confusus and C. beldingi commonly occupy the same river system, they rarely

overlap longitudinally.

3) Local - separation within a longitudinal section of river. Although several studies have examined localized segregation of lentic species (e.g., Werner 1977; Werner et al. 1977), there is very little quantitative evidence of local interactive segregation by stream fishes. Many individual species, however, are qualitatively known to inhabit only pools or riffles and may thus be separated from other species.

The species distributions given by Bond (1963) indicate that the Cottus species of northwestern North America offer examples of species segregation on each of the spatial scales of resolution. Several endemic forms are geographically separated from other species. In most cases this separation is, however, the result of biogeographic barriers and is of little direct interest in the ecology of the species. Most sculpins, including Cottus perplexus, C. rhotheus, and C. beldingi, broadly overlap in geographical distribution. Their longitudinal and local patterns of distribution thus become of major interest.

METHODS

The Study Site

The principal study site for the investigation of interactive segregation in a guild composed of Cottus perplexus, C. rhotheus, and C. beldingi was the portion of the Marys River system, Benton and Lincoln Counties, Oregon, upstream of Philomath (Fig. 2). The river was selected for its accessibility and because it offers a variety of tributaries with different environmental conditions.

The Marys River system is part of the Willamette River drainage. It flows from the Coast Range east to meet the Willamette River at Corvallis. The drainage area upstream of Philomath is approximately 400 km² (U. S. Geological Survey 1976); within this area the river drains both forested and agricultural land. The tributaries draining Marys Peak (Shotpouch Creek, Woods Creek, Rock Creek) flow primarily from coniferous forest. Other portions of the system drain farm land, although in most reaches there is some deciduous riparian vegetation. Tributaries also differ considerably in gradient and predominant substrate (Fig. 3). The tributaries draining Marys Peak are high gradient streams with primarily rocky substrates, but the headwaters above Blodgett are low gradient and contain nearly totally fine substrate material. Stream widths within the study area average from less than 1 m in headwater areas to approximately 10 m in the main river at Philomath.

The climate in the area is mild; rainfall averages approximately 100 cm annually (Jensen 1957). Most precipitation, however, occurs in

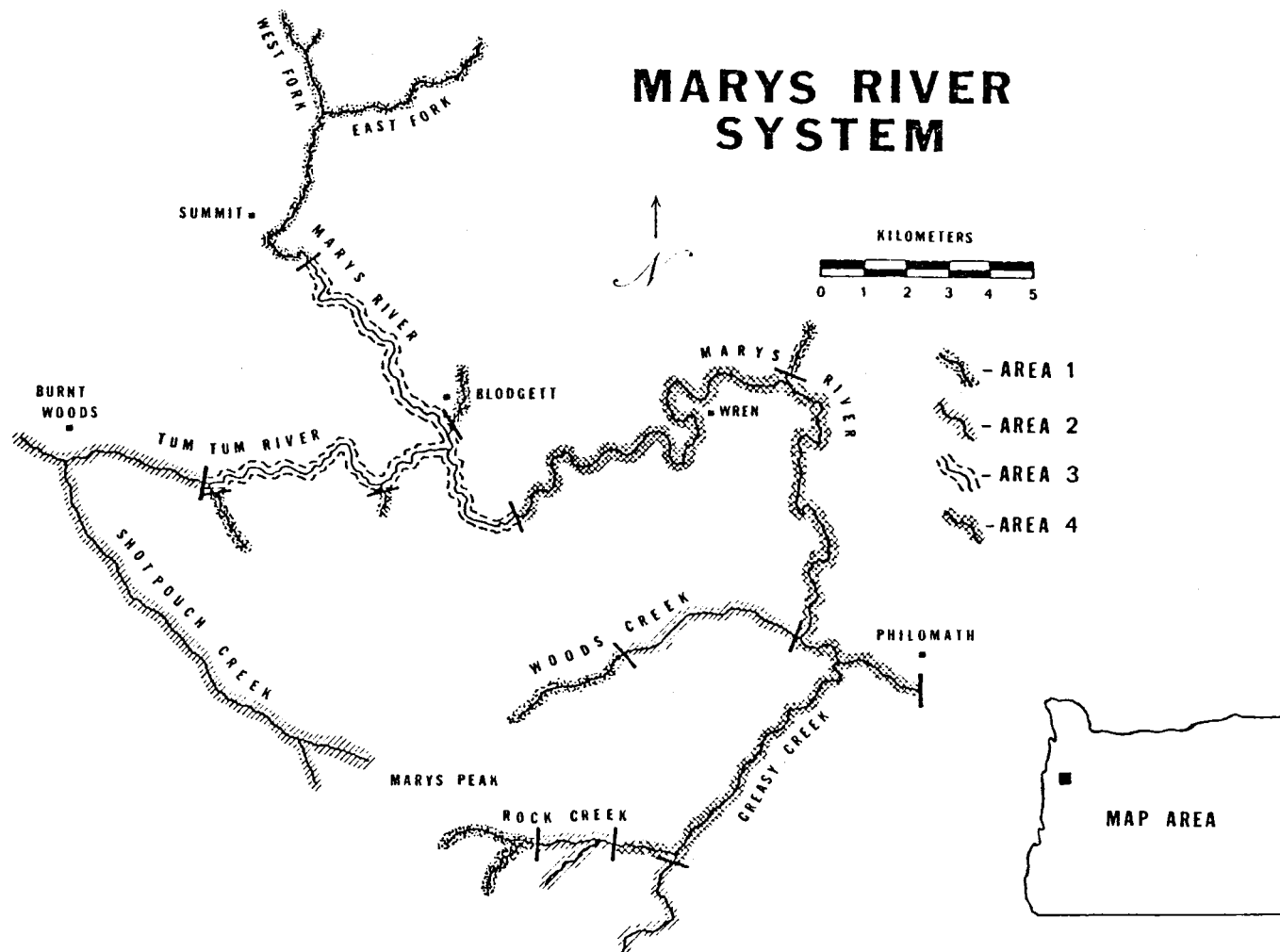


Figure 2. The Marys River system, Benton and Lincoln Counties, Oregon. See text for explanation of area delineations.

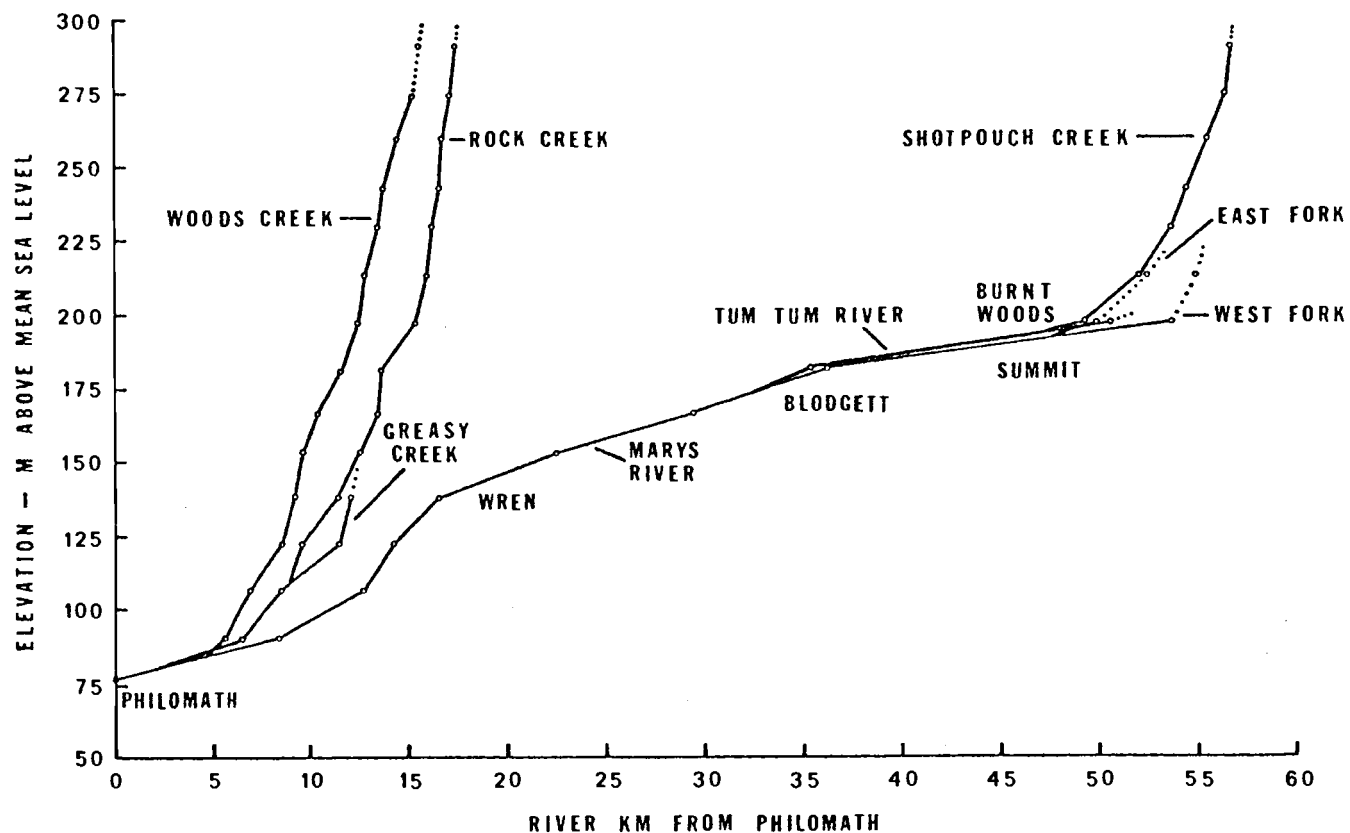


Figure 3. Gradient map of the Marys River system, Benton and Lincoln Counties, Oregon. Data obtained from U. S. Geological Survey 15 minute topographic maps, Corvallis, Monroe, and Marys Peak quadrangles.

the winter months, resulting in strong seasonal patterns in stream discharge. The Marys River at Philomath typically reaches its lowest levels in late summer ($0.25 \text{ m}^3/\text{sec}$); the rapid initial onset of winter rains usually results in a sudden increase to winter water levels (approximately $180 \text{ m}^3/\text{sec}$) in mid-November (U. S. Geological Survey 1976).

Because the Marys River system drains Marys Peak, the highest point in the Oregon Coast Range, it is the only Coast Range tributary of the Willamette River to regularly receive snow-melt water. As a result, its water temperatures can be expected to be somewhat cooler than most rivers in the area, although temperatures at Philomath have been recorded as high as 27° C (pers. obs.). Water chemistry appears to be similar to most Willamette drainage streams; pH is approximately 7.8 (Dimick and Merryfield 1945).

Preliminary Survey

To determine the species composition of the fish fauna, the longitudinal range of each species, and the general longitudinal trends in environmental conditions, a preliminary survey was conducted from June to August, 1977. Approximately 30 sites scattered throughout the river system were sampled with either a small, 5-mm square-mesh seine or a 400-volt pulsed-DC backpack shocker. Although no attempt was made to quantify species abundances, the relative abundance of each species and general environmental conditions (water level, stream width, water temperature, current

velocity, and prevalent substrate) were recorded at each station. Most fish specimens were identified in the field and released.

Local Patterns of Habitat Utilization

The local patterns of habitat utilization and the resulting structure of the benthic vertebrates guild were analyzed with regard to the relative importance of predation, competition, and environmental variability as factors influencing these patterns. Samples, therefore, were distributed in time and space to provide data sets for different combinations of coexisting species (to assess the effects of predation and competition) and different seasons (to assess the effects of environmental variability).

To provide data sets for different combinations of coexisting species, the river system was longitudinally divided into four areas based on the longitudinal distributions of the Cottus species as determined in the preliminary survey. These distributions resulted in areas with one, two, and three coexisting sculpin species. The two species area was further subdivided into small and large stream areas when preliminary work indicated that different patterns of species interactions occurred in these distinct environments. The four study areas shown in Figure 2 were therefore delineated as:

Area 1: C. perplexus alone

Area 2: C. perplexus and C. rhotheus, small stream

Area 3: C. perplexus and C. rhotheus, large stream

Area 4: C. perplexus, C. rhotheus, and C. beldingi

The data obtained from all sample sites within each of these areas were combined for analysis.

To provide data sets for different seasons, the year was divided into discrete seasons based on water levels and species breeding habits. Because the sudden onset of winter rains in the region typically results in a rapid rise in water levels in mid-November (U. S. Geological Survey 1976), the following seasonal classification was used in preference of calendar seasons:

Summer: July 1 to November 14, low water levels

Winter: November 15 to March 31, highwater levels

Spring: April 1 to June 30, breeding season, moderate
water levels

The data obtained from each area within each of these seasons were combined for analysis. Because both the area and seasonal classifications had somewhat artificial limits, sampling near both spatial and temporal boundaries was avoided.

Sampling to determine local habitat utilization required consideration of measureable environmental variables that reflect local spatial heterogeneity. Temperature, oxygen, and other dissolved substances rarely exhibit local gradients in streams (Hynes 1970); they were therefore not considered pertinent environmental variables on a local scale of resolution. Major local differences may occur, however, in current velocity, depth, substrate, and distance to the shore; these variables were therefore selected as the major environmental factors that reflect local spatial heterogeneity.

The benthic habits of sculpins and the local variability in physical environmental conditions required the use of a number of fish sampling techniques. The ability of sculpins to seek cover under rocks often makes electrofishing rather ineffective and biased toward the capture of species that are less prone to burrow. Similarly, active seining is frequently ineffective as the lead line of the net often rides over rock crevices into which sculpins have retreated. The kick net, a small bag seine suspended on a metal frame and used passively, is considerably more effective and less selective. The net is positioned on the bottom while the substrate directly upstream is disturbed by kicking. The technique does, therefore, require a current to carry the fish into the net. After a preliminary examination of the effectiveness of kick netting and electrofishing, the kick net was determined to be suitable where the current velocity near the substrate exceeded 0.1 m/sec; any such area was defined as a riffle. In areas where the current velocity near the substrate was less than 0.1 m/sec, defined as pools, electrofishing was used in conjunction with a diligent search of the bottom for stunned sculpins hidden under rocks. During most seasons, the smooth water surface and water clarity in pools allowed this search to be effective.

Local sampling in riffles was carried out on a 1-m^2 scale of spatial resolution. For each riffle sample, a kick net of 5-mm square mesh was quietly positioned on the substrate. The mouth of the net was approximately 1 m wide; 1 m was paced off directly

upstream to delineate a 1-m^2 sample area. The substrate within the square meter was then thoroughly disturbed by kicking for 20 seconds. All fish caught were identified to species, measured for standard length, and released. The net was then removed and physical environmental variables measured. Stream width and distance from the nearest shore to the center of the square meter were measured with a steel tape or meter stick. Current velocity was measured with a Gurley Pygmy Current Meter suspended on a metal shaft approximately 2 cm from the substrate; preliminary work indicated that a reading at this depth was a better characterization of the site in terms of benthic fish distributions than was the standard reading of the average current velocity in the water column at 0.6 depth (Hynes 1970). Current velocity was measured at both sides and in the center of the square meter approximately 0.5 m upstream from where the mouth of the kick net had been positioned. For analysis, the sample was categorized by the arithmetic mean of the three current velocity readings. Depth was measured with a meter stick at the same locations as current velocity; the sample was also categorized by the arithmetic mean of the three depth readings.

To quantify the composition of the substrate within the square meter, the percentage of the area covered by patches of different substrate materials and the size range of the particles comprising each patch were estimated by eye. English units were used for all size determinations as they were assumed to be more reliable than metric units for this estimation; they were later converted to metric

units. The presence and percent cover of any vegetation or debris were also noted. This description was then used to calculate an arithmetic mean substrate particle size for the sample. The percent cover of vegetation and debris was not considered in this calculation, but was related separately to fish abundance.

Pools were sampled with a 400-volt pulsed-DC backpack shocker. An area of approximately 5 to 20 m² with current velocity near the substrate less than 0.1 m/sec was selected and shocked. One pass through the area was made while the bottom was thoroughly searched for stunned sculpins hidden under rocks. Fish captured were identified to species, measured for standard length, and released. The site was then measured with a metal tape to determine its exact area; the distance from the shore to the edges of the area were also measured. Depth was measured with a meter stick at approximately 2 m intervals along transects dissecting the site; the total number of readings depended on the size of the area. The site was categorized by the arithmetic mean of the depth readings. The composition of the substrate was estimated by eye and a mean substrate particle size for the site was calculated with the same methods employed for riffle sampling. The density of fish at the site was converted to a m² figure by dividing the number of each species caught by the area of the sample.

A total of 750 m² of riffles and 306.3 m² of pools was sampled in this manner. The apportionment of the samples among areas and seasons and a sample field data sheet are shown in Appendix I. To minimize

the effects of sampling on the natural patterns, no individual site was sampled more than once a season. At each site an attempt was made to distribute samples over the full range of available habitat; the range and distribution of the measured environmental variables were therefore assumed to reflect their availability in each area. Samples were analyzed as they were accumulated; within each area in each season sampling was continued until a pattern of habitat utilization emerged. Generally, this resulted in taking more samples in the multispecies areas. Full sets of pool and riffle samples were taken in summer and spring; in winter Area 3 was totally inaccessible due to high water levels. Similarly, no quantitative pool samples could be taken in any area in winter because turbid water obscured the bottom.

Winter patterns in pools, as well as the more general patterns of habitat utilization during all seasons, were, however, qualitatively examined. In each area in each season, large sections of the stream were electrofished with the backpack shocker. At each site both pools and riffles were sampled. Fish captured were identified to species, measured for standard length, and released; the pattern of habitat utilization by each species was qualitatively noted.

Due to the 5-mm mesh size of the kick net and the inability to see very small fish when shocking, the use of habitat by sculpin larvae in the spring could not be quantitatively examined. These patterns were, however, qualitatively evaluated. During the spring

a thorough search was made of both pools and riffles in each area with a 1.25-mm square-mesh aquarium net suspended on a 25-cm by 17-cm wire frame. In pools the net was dragged along the substrate. In riffles it was held in place on the substrate while the bottom immediately upstream was disturbed by hand. The stage of development of the larvae captured and their use of different portions of the stream were qualitatively noted.

For the analysis of local patterns of habitat utilization, the quantitative samples were examined on several scales of resolution. On a pool-riffle scale, patterns across areas and seasons were examined separately for pools and riffles. Sculpin densities in pools and riffles could not be directly compared because these environments were sampled with different types of fish collection gear with dissimilar capture efficiencies. Within riffles, local use of habitat was evaluated on a finer scale of resolution. The density of each sculpin species was examined across areas and seasons as a function of current velocity, depth, mean substrate particle size, and distance to shore. The overlap measure of Levins (1968) as modified by Pianka (1973) was used to calculate the within-riffle overlap between species along each of these environmental variables separately:

$$\alpha_{ij} = \frac{\sum_{k=1}^n p_{ik} \cdot p_{jk}}{\sqrt{\sum_{k=1}^n p_{ik}^2 \cdot \sum_{k=1}^n p_{jk}^2}}$$

where: p_{ik} = the portion of the distribution of
species i in the k^{th} subdivision of
the environmental variable,

and; n = the number of subdivisions of the
environmental variable.

This measure was considered merely as a method of summarizing the overlaps of the distributions and was not viewed as a measure of competition between the species (for discussion, see Colwell and Futuyama 1971; Vandermeer 1972; May 1975). Further, this measure was restricted to within-riffle overlap. The numerical densities of pool and riffle samples could not be directly compared; measures of overlap including both pools and riffles therefore could not be calculated.

The total within-riffle overlap along all four environmental variables simultaneously was examined in two ways. The total overlap was quantified as the product of the four univariate overlaps after Cody (1974). Although this method was considered adequate as a summary of total overlap, May (1975) noted several possible drawbacks to this technique. Multivariate patterns of overlap were therefore also examined by calculating a principal components ordination of the environmental data from the 750 riffle samples. The environmental data were standardized (zero mean, unit variance) and principal component scores were calculated for each sample. The samples for each area in each season were then plotted separately in principal component space (for methods, see Cooley and Lohnes 1971; Cassie

1972). The distribution of each species was superimposed on these ordinations.

Preliminary analysis revealed that habitat utilization by each species changed over its life span; the major change occurred after the first year of life. Further, the rapidly changing catchability of the young-of-the-year as they grew throughout the spring and summer added considerable variability to the numerical density data. Accordingly, approximate ranges in length for the young-of-the-year for each species in each season were estimated from length-frequency plots. Calculations of numerical densities were then made separately for young-of-the-year and adults.

Weight-length relations developed from specimens collected during the preliminary survey were used to calculate biomass from standard lengths measured in the field. Upon collection, specimens were immediately placed in 10% unbuffered formalin and transferred to 45% isopropanol approximately two weeks later. Approximately one year after collection, 30 specimens of each species from sites along the length of the river system were removed from the preservative, blotted dry for approximately 20 seconds, and weighed. The wet weights of 12 live specimens of each species were compared to those of the preserved specimens. Because no significant differences were found between the live and preserved weights, the weight-length relations developed from the preserved weights were considered appropriate for biomass calculations.

Artificial Stream Experiments

In the field, samples were distributed among the four study areas to provide data sets for different combinations of coexisting Cottus species. This design was used to assess the effects of species interactions on local patterns of habitat utilization and the resulting guild structure. Connell (1975) noted, however, that such a sampling plan can be criticized on the grounds that the areas may differ in factors other than the combination of coexisting species. Perhaps the most likely alternative explanation of changes in the local patterns of habitat utilization among areas is that the sites are physically different. To alleviate this flaw in the field sampling design, local habitat utilization by different combinations of coexisting C. perplexus, C. rhotheus, and C. beldingi was examined in an artificial stream that provided a constant environment.

Access to four identical stream troughs, each approximately 9.1 m long, 1.2 m wide, and 0.6 m deep, was provided by the Oregon State University Oak Creek Laboratory of Biology. Each stream contained a plexiglass wall along one side for direct observation and was arranged to contain a shallow riffle grading into a deep pool. The substrate in the riffles was cobble-sized gravel; that in the pools was fine sand with one large rock for cover. Each pool and riffle also contained one partially submerged log. Water was recirculated through the streams at approximately $0.015 \text{ m}^3/\text{sec}$; it was replenished at 20 l/min from an unfiltered natural surface source.

The streams were placed into operation approximately three months before the experiments began. Colonization by plants and animals was allowed to proceed naturally from the unfiltered water source and from eggs deposited by flying insects. By the time the experiments began, sizeable populations of insects (primarily Ephemeroptera and Diptera) and growths of algae were present in each stream.

Each of the four streams was divided into 14 sections approximately 0.6 m long. For analysis, each section was categorized by its current velocity, depth, and substrate. The same measurement techniques employed in field sampling were used, except that three current velocity and depth readings were made at each section boundary at 0.3 m intervals across the stream. Each section was categorized by the arithmetic mean of the six readings measured at both its boundaries.

Access to the streams could only be obtained while a study of the benthic invertebrate fauna was also in progress; the experimental possibilities for my study were therefore limited. All four streams had to receive the same treatment and the substrate could not be drastically disturbed. The latter restriction made it impossible to remove all sculpins of one species after they had been placed into the streams. Species were therefore added to each stream sequentially at one week intervals in the following order: Cottus perplexus, C. beldingi, and C. rhotheus.

On the day a species was to be introduced into the streams, 16 adult specimens of the appropriate species were collected by

electrofishing sites within Area 4 of the Marys River. Each specimen was measured for standard length and weighed; four individuals were then placed into the center section of each stream. For the next three days visual observations of behavior were made at irregular time intervals; both day and night observations were made. Four days after each species was introduced a thorough census of each stream was conducted. Beginning at the upstream end, each 0.6 m section was electrofished with a 400-volt pulsed-DC shocker while a small 5-mm square-mesh seine was held at the downstream boundary. An observer spotted the stunned sculpins through the plexiglass wall. The stream section containing each sculpin captured was noted; the fish was then measured for standard length, placed in a holding tank for recovery, and later released into the section from which it had been captured. The census data from all four streams were combined for analysis. The same methods employed for the field samples were used to examine the numerical density of each species as a function of current velocity, depth, and mean substrate particle size.

RESULTS AND INTERPRETATION

Composition of the Vertebrate Fauna

During the course of this study, 12 fish species were captured in the Marys River system above Philomath. The three sculpin species that are the focus of this study, Cottus perplexus, C. rhotheus, and C. beldingi, were by far the most common vertebrates within the study area. The remaining nine fish species collected were considerably less abundant; most were confined to pools and stream margins. Ammocoetes of two lamprey species, Lampetra richardsoni and L. tridentata, were commonly observed in sand and silt substrates in pools. Adults of L. richardsoni were occasionally collected throughout the area; adult L. tridentata were observed only during their spring spawning migration. Small cutthroat trout, Salmo clarki, generally less than 20 cm in length, occurred throughout the river system, but were common only in the headwater areas of Shotpouch Creek, Woods Creek, and Rock Creek. Small numbers of the mountain whitefish, Prosopium williamsoni, apparently move into the river during the winter; one mature individual was captured in the main river approximately 3 km below Blodgett. The northern squawfish, Ptychocheilus oregonensis, and the largescale sucker, Catostomus macrocheilus, were very uncommon within the study area; the only specimens captured were juveniles and were confined to pools in the downstream reaches of the Marys River. The sand roller, Percopsis transmontana, was also uncommon and was confined to pools over sand

and silt substrates. The redbside shiner, Richardsonius balteatus, and the blackside dace, Rhinichthys osculus nubilus, were the most common species present other than the sculpins. The redbside shiner was found in pools throughout the study area, but was more common in downstream reaches. The blackside dace was somewhat more common than the redbside shiner and also occurred throughout the study area. Juvenile blackside dace were restricted to pools. Adults moved into fast-flowing, rocky riffles in spring, apparently for spawning, but were found mainly in pools during the remainder of the year.

Several fish species that had been previously reported from this portion of the drainage were not observed and may no longer exist in the river system. The chinook salmon, Oncorhynchus tshawytscha, and the coho salmon, O. kisutch, have been reported to stray into the Marys River only rarely (Dimick and Merryfield 1945). Hatchery stocks of both species have been introduced into the drainage but apparently have not been successful (C. E. Bond, pers. comm.). The capture of small numbers of the mountain sucker, Catostomus platyrhynchus, in the pools of lower Greasy Creek was reported by DeHart (1975). The mottled sculpin, Cottus bairdi, is known from the drainage only from one specimen collected from Rock Creek (Bond 1963). If it does still exist in the river system it is too rare to have any significant effect on the Cottus species interactions studied in this thesis.

In addition to the 12 fish species captured during the course of this study, salamanders of the genera Taricha and Dicamptodon were infrequently observed. Both were extremely uncommon within the study

area and were restricted to extreme headwater areas.

Longitudinal Distribution of Cottus species

The preliminary survey revealed that the patterns of longitudinal distribution were markedly different for the three Cottus species. Cottus perplexus occurred throughout the river system, but was most common in headwater areas or small tributaries where it existed alone. Although C. rhotheus did occur far upstream in Shotpouch Creek, it was generally found only in the middle and lower reaches of the river system. Cottus beldingi had the most restricted distribution within the study area; it occurred only in the lower reaches. These distributions are summarized by the area delineations of Figure 2: C. perplexus was found in all areas; C. rhotheus existed in Areas 2, 3, and 4; C. beldingi was found in Area 4 only.

The longitudinal distributions of these species were most directly related to the predominant substrate material in riffles and not to the other environmental variables that also vary longitudinally. Limits in species distributions, delineated by the area boundaries, do not coincide with either major changes in gradient or the confluence of major tributaries (Figs. 2, 3). Similarly, although species temperature tolerances are often suspected of influencing the longitudinal distribution of stream fishes (e.g., see Hynes 1970), maximum temperatures within the study area were below the lethal

limits of all three species (see Appendix II and DeHart 1975). In fact, C. rhotheus and C. beldingi, which are less tolerant of warm water than C. perplexus (Bond 1963; DeHart 1975), occurred in the warmest reaches within the study area. Species boundaries did, however, generally coincide with major changes in the mean substrate particle size, especially that in riffles (Table 1). Area 1, where C. perplexus existed alone, is dominated by fine sand, silt, and clay substrates. Cottus rhotheus was not present in this area, but

TABLE 1. Mean substrate particle size for each area, Marys River, Oregon. Values represent the means of all substrate data obtained during the fine resolution sampling in each area.

Area	Mean Substrate Particle Size (cm)	
	Riffles	Pools
1	2.90	0.00+
2	6.66	13.80
3	12.42	8.18
4	8.17	6.18

occurred in Areas 2, 3, and 4 where the substrate is primarily rocky. The riffles of Area 3, however, differ from those of Areas 2 and 4 in that the mean particle size is larger and the rocks are often imbedded in finer substrate material. Cottus beldingi did not occur in Area 3, but was common in Area 4 where most riffles contain loose, cobble-sized rocks with many interstitial spaces. Although the riffles of Area 2 also appear suitable for C. beldingi, this species

was not found in this area. The distribution of C. beldingi may be related to unknown factors associated with the smaller stream widths of Area 2, or, in the case of the Shotpouch Creek portion of Area 2, may be due to the inability of C. beldingi to colonize the area. To do so it would have to pass through many miles of unsuitable environment in Area 3.

The longitudinal pattern of sculpin distributions in the Marys River system above Philomath therefore appears to be most strongly related to riffle substrate characteristics and, within the length of the river system studied (approximately first- through fifth-order streams), is a pattern of species addition downstream rather than one of sequential longitudinal replacement. The three sculpin species therefore do not separate on a longitudinal scale of resolution. Possible separation within local sections of river must consequently be considered.

Local Patterns of Habitat Utilization

The three species of Cottus exhibited markedly different patterns of habitat utilization within local sections of the river system. These patterns appear to be related to the breadth of environmental tolerance of each species and the presence or absence of other Cottus species. Data pertaining to these patterns will first be examined on a pool-riffle scale of resolution (Table 2). Only adults (age I and greater) are considered in this table because the influx of young-of-the-year in spring and their change in catchability with growth

TABLE 2. Numerical densities of sculpins (Cottus), Marys River, Oregon. Young-of-the-year have been excluded from these data. Riffle data from kick net sampling; pool data from electrofishing sampling.

Habitat	Season	Numerical density (no./m ²)							
		Area 1	<u>C. perplexus</u>		Area 4	<u>C. rhotheus</u>			<u>C. beldingi</u> Area 4
			Area 2	Area 3		Area 2	Area 3	Area 4	
Riffles	Summer	1.12	0.19	0.02	0.00	0.64	0.33	0.19	0.20
	Winter	0.50	0.22	--*	0.02	0.30	--*	0.11	0.38
	Spring	1.16	0.38	0.03	0.07	0.56	0.43	0.34	0.34
Pools	Summer	1.79	1.20	0.25	0.21	0.30	0.05	0.03	0.00
	Winter	--*	--*	--*	--*	--*	--*	--*	--*
	Spring	1.59	1.17	0.50	0.60	0.04	0.04	0.00	0.00

* Riffle sampling in Area 3 and all quantitative pool sampling impossible in winter due to high water levels and turbidity.

during the remainder of the year would add considerable variability to these data.

In all seasons, C. perplexus was abundant in Area 1, where it existed alone. In this area, C. perplexus demonstrated a slight preference for pools, although riffles were also used extensively. Density in Area 1 riffles was lowest in winter. Although there are no corresponding quantitative data for pools in winter, qualitative sampling revealed that C. perplexus did tend to utilize pools to a greater degree during the winter periods of high water levels. This decrease in riffle density in winter was, however, also due to dilution. The small streams of Area 1 drastically increased in surface area during winter flooding; this increase effectively reduced sculpin density. Cottus perplexus therefore did not demonstrate a strong pool or riffle preference in Area 1. Rather, the sculpins tended to be found where the most cover was available, regardless of whether the cover was associated with flowing or still water. In some sections of Area 1 (e.g., upper Woods Creek), cover was provided by the rocky substrate. In the Marys River above Blodgett, however, the substrate was too fine to furnish cover; the only hiding places were provided by vegetation and wood debris. In this portion of the drainage the numerical density of C. perplexus was correlated with the amount of cover in both pools and riffles (Fig. 4). The relation was considerably stronger in riffles, however, suggesting that the greater depth of pools made the need for cover less significant.

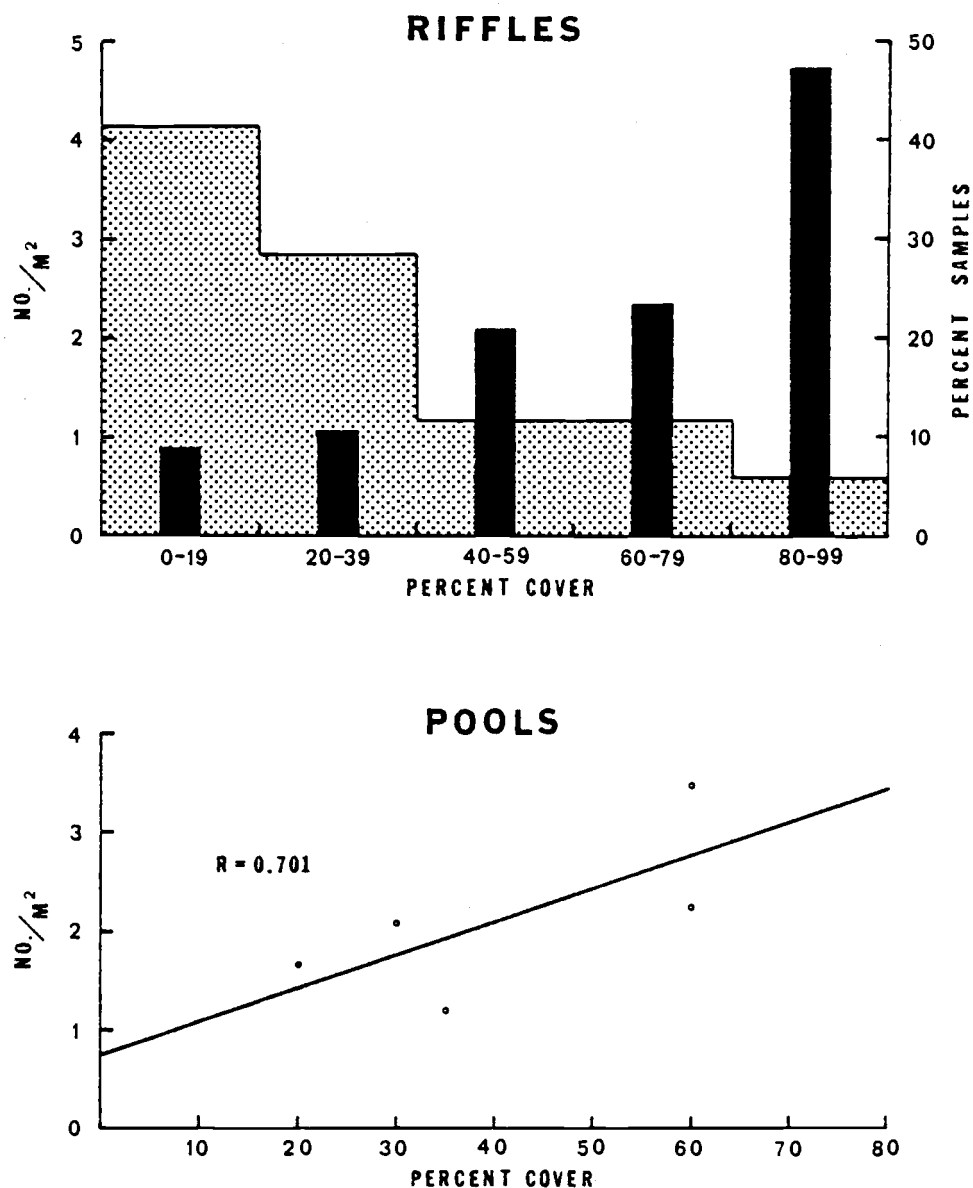


Figure 4. Numerical density of Cottus perplexus in the upper Marys River, Oregon, in relation to cover provided by vegetation and wood debris. In the riffle plot, black bars represent numerical densities; stippled area represents the distribution of samples. The distribution is significantly different from a uniform distribution at $P < 0.005$ ($\chi^2 = 43.97$; d.f. = 4). The correlation coefficient in the pool plot is significant at $P = 0.11$. In both cases, data from all seasons were combined.

In Areas 2 and 3, where C. perplexus coexisted with C. rhotheus, the density of C. perplexus was considerably less than that of Area 1, especially in riffles (Table 2). In both areas, C. perplexus was primarily found in pools. This pattern was also prevalent in Area 4, where C. perplexus coexisted with C. beldingi as well as C. rhotheus. The exclusion of C. perplexus from riffles was, however, much more marked in Areas 3 and 4 than in Area 2. Because the patterns in Areas 3 and 4 were similar, the addition of C. beldingi did not appear to affect the local distribution of C. perplexus. The patterns in Areas 2 and 3 strongly differed, however, although both areas contained only C. rhotheus and C. perplexus. Area 2 differed from Area 3, however, in that the streams in Area 2 were narrower and, perhaps as a result, the size composition of the C. rhotheus population was quite dissimilar from that of Area 3. In Area 2, where the exclusion of C. perplexus from riffles was not as pronounced, only 6.8% of the C. rhotheus population was greater than 80 mm in standard length. In Areas 3 and 4 this figure was 9.5% and 16.5%, respectively. These patterns therefore appear to be related to different rates of competition and predation exerted by C. rhotheus on C. perplexus in the three areas. All sizes of C. rhotheus may compete with C. perplexus; strong predation, however, can only be exerted by the larger C. rhotheus. The partial exclusion of C. perplexus from the riffles of Area 2 may therefore be due to competition and a small amount of predation by C. rhotheus; in Areas 3 and 4 the nearly total exclusion of C. perplexus from riffles may

be due to competition plus a greater amount of predation exerted by the greater numbers of large C. rhotheus. In all areas C. perplexus finds a refuge from competition and predation in pools because both C. rhotheus and C. beldingi are primarily riffle dwellers.

Seasonal patterns and their relation to changes in resource abundance provide further support for this argument. The density of C. perplexus in riffles in Area 2 was higher in spring than in winter or summer. This may be partially due to individuals moving into the riffles to spawn; many of the C. perplexus captured in riffles in spring, however, did not appear to be in spawning condition. The greater density of C. perplexus in riffles in spring may therefore indicate that increased food abundance during spring eased competition between C. perplexus and C. rhotheus and resulted in a greater penetration into riffles by C. perplexus. Although C. rhotheus, especially the larger individuals, do prey on fish, the primary food of all sculpins is aquatic insect larvae. Although there are no published reports of seasonal changes in insect biomass in the Marys River within the study area, in nearby Oak Creek and Berry Creek the insects that can be expected to comprise most of the food of sculpins (Ephemeroptera, Plecoptera, Trichoptera) have been shown to emerge primarily in late spring and early summer (Kraft 1963; Anderson and Wold 1972; Kerst and Anderson 1974). The maximum biomass of the immature aquatic stages in the stream can therefore be expected to occur in spring just before most emergence takes place. Qualitative observations on the Marys River system within the study area support

this pattern. In spring many larval Ephemeroptera, Plecoptera, and Trichoptera were captured in the kick net samples. By late summer their abundance had dropped dramatically, especially that of the larger Ephemeroptera. The abundance of food in spring therefore may have lessened competition and allowed C. perplexus to penetrate farther into riffles in Area 2. This effect did not, however, occur to a significant extent in Areas 3 and 4, although numerical densities of C. perplexus in riffles in these areas were slightly higher in spring than in summer or winter. Apparently, the increase in food abundance was not sufficient to significantly ease the greater predation on C. perplexus exerted by C. rhotheus in these areas.

In all areas, C. rhotheus occurred primarily in riffles; significant numbers of this species entered pools only in Area 2 in summer (Table 2). This movement to pools may also be related to late summer food scarcity. At this time individuals may be forced to wander more in search of prey. Although summer pool densities of C. rhotheus in Areas 3 and 4 were slightly higher than those of spring, the pattern was not as pronounced as in Area 2. In the larger streams of Areas 3 and 4 the influx of C. rhotheus may be diluted by the larger size of the pools. There may also be a tendency for C. rhotheus to enter pools to a greater extent in small streams where the distance to the pools from their preferred riffles is shorter. Qualitative observation indicated that C. rhotheus usually moved through pools for short time periods before returning to riffles; this pattern is facilitated where small pools are interspersed with

many riffles, as is the case in Area 2.

Seasonally, the density of C. rhotheus in riffles was lower in winter than in spring or summer. The greater volume of flow and the resulting more rapid current velocities in winter may have forced this species out of many riffle areas.

In the Marys River, C. beldingi was found only in riffles; during the entire course of this study no individuals were captured in pools (Table 2). Numerical densities of C. beldingi varied seasonally in a pattern opposite that of C. rhotheus; maximum density occurred in winter, minimum density occurred in summer.

Qualitative sampling indicated that patterns of habitat utilization by larval sculpins were similar to those discussed above for adults. In Area 1, larval C. perplexus were captured primarily in pools, but were also occasionally found in riffles. The greatest densities of larvae occurred in the open over silt substrates. Vegetation and other cover was avoided, perhaps due to the concentrations of larval Odonata and other predators. In Areas 2, 3, and 4, larval C. perplexus were collected only from pools, again primarily over silt substrates. Greatest densities were found in the sections of pools near adjacent riffles. Larval C. rhotheus and C. beldingi were captured only in riffles. Larval C. rhotheus appeared to prefer finer substrates than the adults of this species, but larval C. beldingi occurred in the same areas as the adults.

Generally, the biomass of each species followed the same patterns across areas and seasons as the numerical density (Table 3). The data

TABLE 3. Biomass of sculpins (*Cottus*), Marys River, Oregon. Riffle data from kick net sampling; pool data from electrofishing sampling. Biomass calculated from standard lengths with the weight-length relations shown in Appendix IV.

Habitat	Season	Biomass (gm/m ²)							
		Area 1	<i>C. perplexus</i>		Area 4	<i>C. rhotheus</i>			<i>C. beldingi</i> Area 4
			Area 2	Area 3		Area 2	Area 3	Area 4	
Riffles	Summer	2.041	0.518	0.046	0.002	2.500	1.399	1.592	0.464
	Winter	1.704	0.632	--*	0.087	1.964	--*	1.272	1.404
	Spring	2.037	0.727	0.176	0.106	2.322	1.937	2.811	1.376
Pools	Summer	3.519	2.414	0.489	0.444	3.572	0.363	0.070	0.000
	Winter	--*	--*	--*	--*	--*	--*	--*	--*
	Spring	1.833	1.823	0.964	1.359	0.301	0.090	0.000	0.000

* Riffle sampling in Area 3 and all quantitative pool sampling impossible in winter due to high water levels and turbidity.

do, however, add several points to the previous discussion. In the riffles of Area 2, both the numerical density and biomass of C. perplexus were greater in spring than in summer or winter. This seasonal increase was, however, considerably more pronounced in numerical density than in biomass, indicating that the individuals captured in riffles in spring were not exclusively the larger, breeding C. perplexus, but also included many smaller, immature sculpins. The data therefore lend further support to the hypothesis that the greater penetration of C. perplexus into the riffles of Area 2 in spring was not merely a breeding movement, but was in part due to a relaxation of competition. Similarly, the biomass of C. rhotheus was generally low in pools, but not as low as expected from the numerical density. This suggests that the larger C. rhotheus were more prone to use pools than were smaller individuals. These large sculpins consume proportionately greater numbers of fish than the smaller C. rhotheus; pools were observed generally to contain the greatest concentrations of small fish, especially Cyprinidae. In C. beldingi, biomass patterns were identical to those seen in the numerical density data. This was expected, as on this scale of resolution all size classes of this species appeared to have similar patterns of use of habitat.

Total sculpin biomass by areas and seasons for all species combined provided further information linking sculpin distributions to the physical characteristics and resource abundance levels in different portions of the environment (Table 4). In riffles, total

sculpin biomass tended to be lower in Areas 1 and 3 than in Areas 2 and 4. As was discussed earlier, the major difference in the physical environment among these areas is the composition of the predominant substrate (Table 1). The riffles of Area 1 are dominated by fine sand, silt, and clay substrates; those of Area 3 primarily contain

TABLE 4. Total sculpin biomass by areas and seasons, all species combined, Marys River, Oregon. Biomass calculated from standard lengths with the weight-length relations shown in Appendix IV.

Habitat	Season	Total Sculpin Biomass (gm/m ²)			
		Area 1	Area 2	Area 3	Area 4
Riffles	Summer	2.041	3.018	1.445	2.058
	Winter	1.704	2.596	-- *	2.763
	Spring	2.037	3.049	2.113	4.293
Pools	Summer	3.519	5.986	0.852	0.514
	Winter	-- *	-- *	-- *	-- *
	Spring	1.833	2.124	1.054	1.359

* Riffle sampling in Area 3 and all quantitative pool sampling impossible in winter due to high water levels and turbidity.

large rocks imbedded in finer substrate material. In contrast, the substrate in the riffles of both Areas 2 and 4 chiefly consists of cobble-sized rock. This type of substrate in riffles therefore appears to have a greater capacity to support sculpins than either very fine or very coarse material. In pools, biomasses were generally less variable among areas than in riffles. Because the

mean substrate particle size varied as much among areas in pools as it did in riffles (Table 1), the data suggest that substrate characteristics in pools are less critical to sculpins than are those in riffles. Pool biomass was generally greatest in Area 2, reflecting the greater numbers of large C. rhotheus utilizing the pools of this area. Pool biomass was also quite high in Area 1, perhaps because the depths of these pools furnish cover that is not provided by the shallow riffles dominated by fine substrate material.

Although the use of different fish capture techniques in pools and riffles prevented a direct, quantitative comparison of these two environments, the data do suggest that in all sections of the river system except Area 1, riffles supported more sculpin biomass than pools. Hynes (1970) noted that in general, riffles contain greater densities of aquatic insect larvae, the primary food of sculpins. The density of these sedentary, benthic fishes that do not feed extensively on stream drift can be expected to be greater in the areas of greatest food concentrations.

The overall pattern of habitat utilization on a pool-riffle scale of resolution was therefore for C. perplexus to utilize most of the environment where it existed alone, for C. rhotheus to exclude C. perplexus partially from riffles, especially where there were more large C. rhotheus, and for C. rhotheus and C. beldingi to coexist in riffles. The pattern of overlap between C. perplexus and C. rhotheus where C. perplexus did penetrate into riffles and the possibility of separation between C. rhotheus and C. beldingi must therefore be

considered on a within-riffle scale of resolution.

The within-riffle relations between the numerical density of each species and the four environmental variables measured during the kick net sampling (current velocity, substrate, depth, distance to shore) indicated that the species primarily segregated in relation to current velocity (Figs. 5 - 7). The species did demonstrate preferences for certain ranges of the other environmental variables, but their distributions in relation to these factors exhibited considerable overlap (Figs. 8 - 16).

Species segregation in relation to current velocity was particularly pronounced in summer (Fig. 5). As was noted on the pool-riffle scale of resolution, C. perplexus was present in riffles in high density in Area 1, moderate density in Area 2, and very low density in Areas 3 and 4. In Area 1, adult C. perplexus used all the available riffle habitat; young-of-the-year, however, were restricted to the slower portions. Although the distributions were not significantly different from uniform distributions, in Area 2 both young-of-the-year and adult C. perplexus tended to use the slower portions of the riffles, the areas with the lowest densities of adult C. rhotheus. In Areas 3 and 4, the virtual exclusion of C. perplexus from riffles precluded the examination of any within-riffle pattern. In both cases only one individual was captured in riffles during the entire season. In Areas 2, 3, and 4, both adult and young-of-the-year C. rhotheus utilized the full range of available currents. Adult C. rhotheus did prefer the more rapid current

Figure 5. Numerical densities of Cottus in summer in relation to current velocity in riffles. White and black bars represent numerical densities of young-of-the-year and adults, respectively; values are read from the left axis. These age classes were separated on the basis of the length-frequency plots shown in Appendix III. Stippled area represents the distribution of samples; values are read from the right axis. Results of a χ^2 goodness-of-fit test comparing each observed distribution to a uniform distribution are also presented: X = insufficient data for test; N.S. = not significant at $P = 0.05$; * = significant at $P = 0.05$; ** = significant at $P = 0.025$; *** = significant at $P \leq 0.01$.

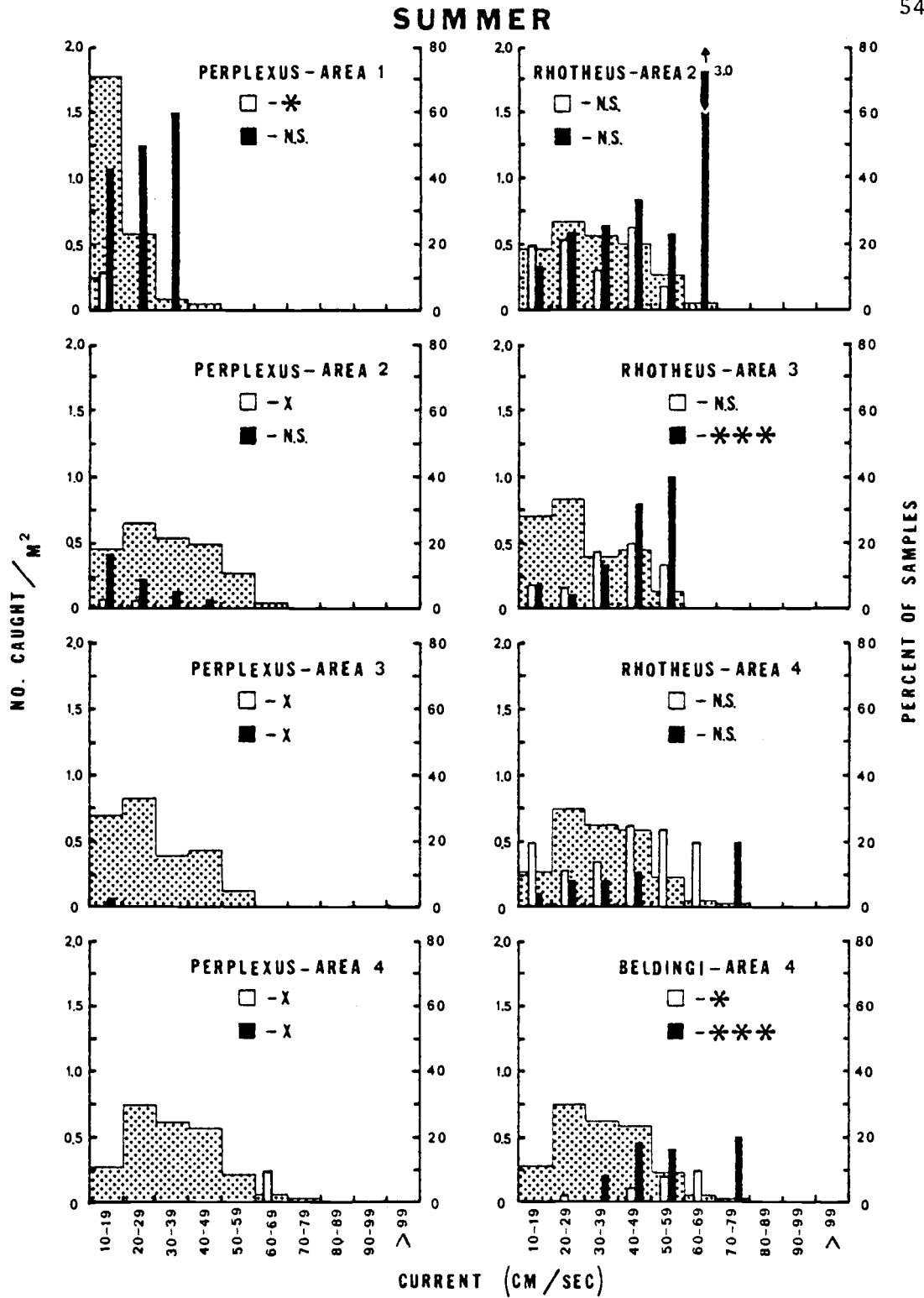


Figure 5.

velocities, although in summer these did not exceed 79 cm/sec. Both young-of-the-year and adult C. beldingi utilized only the more rapid portions of the riffles.

In winter, when larger portions of the riffles in all areas had greater current velocities, the pattern was somewhat different (Fig. 6). The distributions of C. perplexus were similar to those observed in summer, although overall riffle densities were greater in Areas 2 and 4. In the more rapid current velocities of winter, however, C. perplexus, especially the young-of-the-year, preferred the slower portions of the riffles, even in Area 1. In Area 2, both young-of-the-year and adult C. rhotheus again utilized the entire range of currents, although in this area velocities never exceeded 69 cm/sec. In Area 4, where portions of some riffles had very rapid current velocities, C. rhotheus utilized the full range below 69 cm/sec, but was never captured in the more rapid currents. Both the adult and young-of-the-year C. beldingi avoided the slower portions of the riffles and were not found where the current velocity exceeded 90 cm/sec. This species was captured in densities similar to those of summer in current velocities less than 69 cm/sec, but peaked sharply in abundance above that value, the same point that apparently marks the upper current velocity tolerance of C. rhotheus.

The within-riffle distributions of C. rhotheus and C. beldingi therefore appear to be related. An apparent anomaly also exists in that the overall riffle density of C. beldingi in winter is nearly double that of summer (Table 2), although there is no evidence that

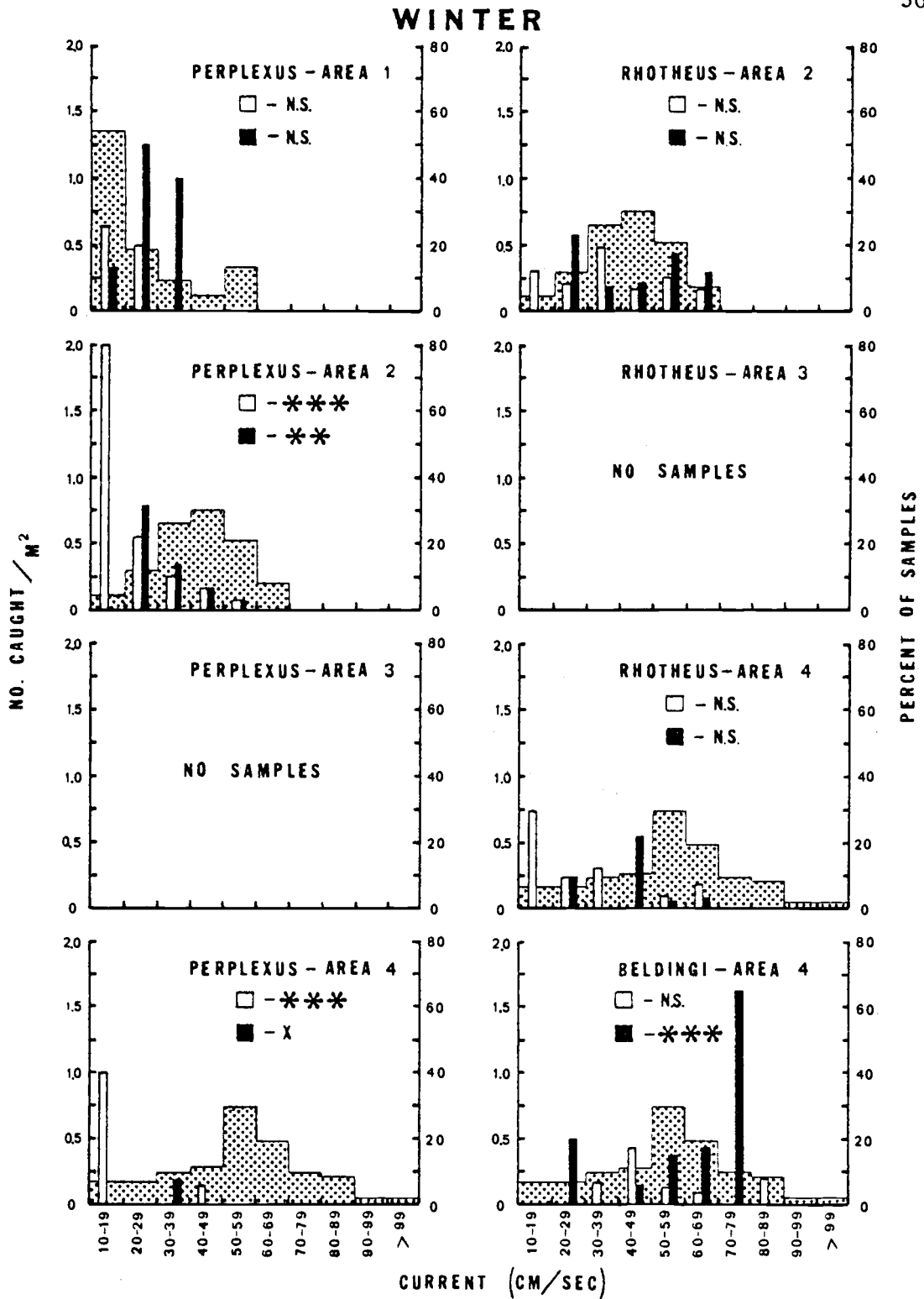


Figure 6. Numerical densities of Cottus in winter in relation to current velocity in riffles. For explanation see legend of Figure 5.

this species moved to pools or undertook longer migrations in summer. The most likely explanation of the pattern is therefore that C. beldingi burrows into the substrate in the presence of C. rhotheus; that C. beldingi has great burrowing ability has already been noted (Bond 1963). The winter data indicate that C. rhotheus has a somewhat lower current velocity tolerance than does C. beldingi. In summer, when all riffles flowed slowly enough to be inhabited by C. rhotheus, C. beldingi was forced into the substrate by predation and competition from C. rhotheus and its catchability with the sampling methods employed decreased. In winter, when the current velocity in some riffle areas exceeded 70 cm/sec, C. rhotheus was forced to move to slower areas. This allowed C. beldingi to emerge from the gravel and greater numbers of this species were captured in the kick net. Although the depth to which C. beldingi burrowed could not be determined, it was sufficient to significantly reduce catchability in the kick net. This sampling method disturbs the first few layers of rock; C. beldingi may therefore retreat a considerable distance into the gravel.

Night sampling during the summer provided further evidence of the burrowing ability of C. beldingi. Although quantitative sampling at night proved to be impractical, qualitative observations revealed a greater density of C. beldingi atop the substrate at night in the same riffles where few had been caught during the day. A tendency for large C. rhotheus to forage in pools and along shallow stream margins at night was also noted. Apparently, the cover

provided by darkness and the movement of some C. rhotheus out of riffles at night allowed C. beldingi to emerge from the gravel and still avoid predation and/or competition from C. rhotheus.

Numerical density patterns in relation to current velocity in spring (Fig. 7) lend further support to the previously discussed hypothesis that competition is eased during this season of food abundance. Cottus perplexus again utilized nearly the full range of available current velocities in Area 1, and also penetrated farther into the faster currents in Area 2 than it did in summer or winter. Cottus perplexus also extended farther into the riffles in Areas 3 and 4 than it did in summer or winter, but the pattern in these areas, where predation by C. rhotheus is apparently more severe, was not as pronounced as in Area 2. In Areas 2, 3, and 4, C. rhotheus again utilized the full range of current velocities under 69 cm/sec. As in winter, C. beldingi reached maximum density above the current velocity limit of C. rhotheus, but was also captured in greater densities than in summer or winter below this limit. As was the case with the increased overlap between C. perplexus and C. rhotheus during the spring, this increased overlap between C. rhotheus and C. beldingi was probably due to C. beldingi emerging from the gravel for breeding and due to relaxed competition between these species during this spring period of food abundance.

Although the species did demonstrate different substrate preferences, their numerical densities in relation to substrate in riffles did not exhibit strong patterns of species separation or

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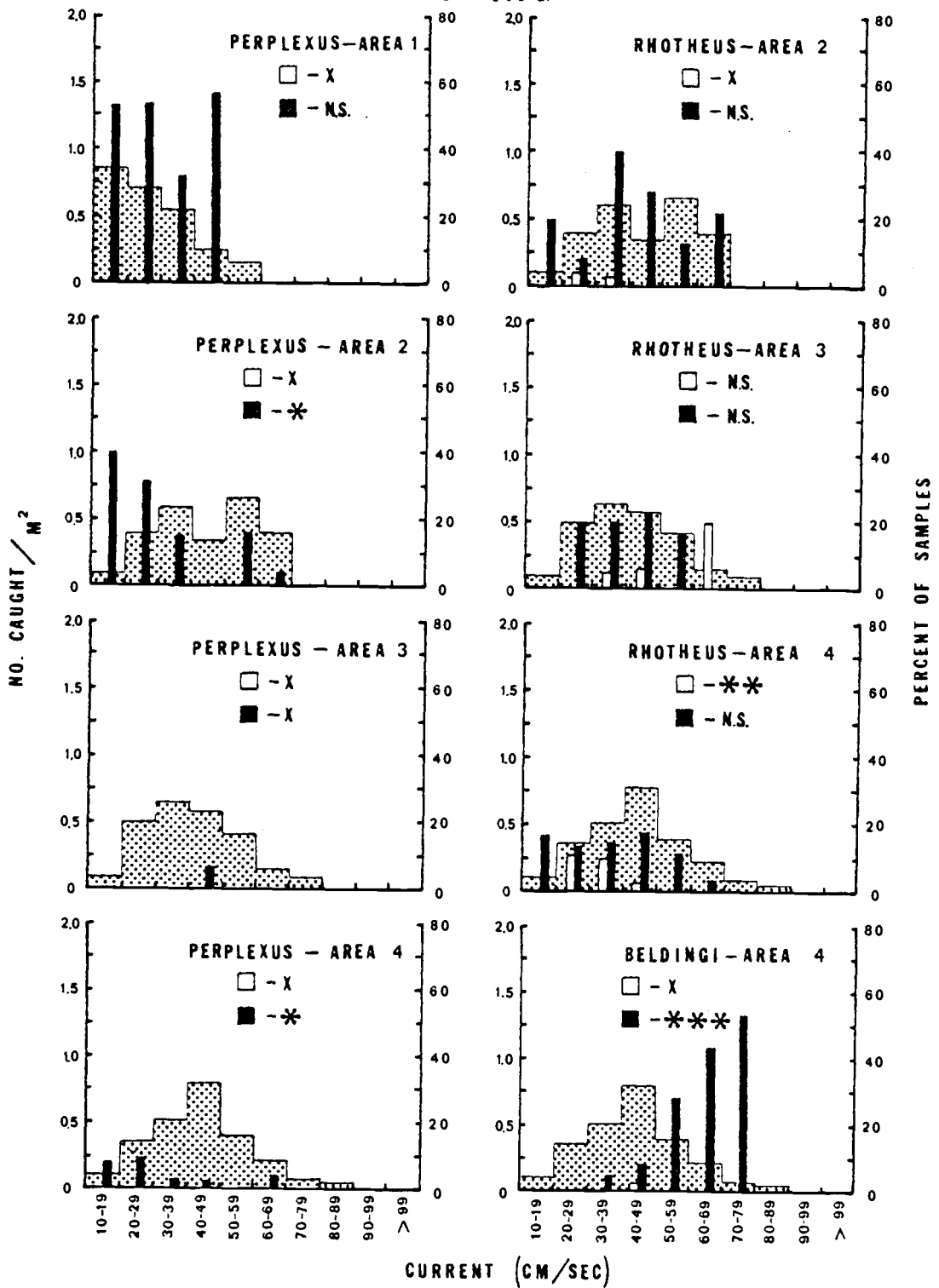


Figure 7. Numerical densities of *Cottus* in spring in relation to current velocity in riffles. For explanation see legend of Figure 5.

shifts in preferences across seasons and areas, as was the case with current velocity (Figs. 8, 9, 10). In all seasons, adult C. perplexus utilized nearly the full range of available substrates; young-of-the-year, however, demonstrated a preference for fine material. Adult C. rhotheus tended to avoid fine substrates, but the young-of-the-year of this species showed a slight preference for the finer material. Both young-of-the-year and adult C. beldingi tended to avoid fine substrates, apparently because they require the interstitial spaces provided by coarser material. The young-of-the-year C. beldingi did utilize finer material to a greater extent than the adults; perhaps the small interstitial spaces furnished by this material are suitable for them but not for the larger adults.

In general, none of the species demonstrated any clear preference for certain ranges of depths, although all tended to avoid the deepest riffle areas (Figs. 11, 12, 13). In summer and winter C. perplexus did, however, exhibit a slight preference for the shallower portions of the streams in those areas where this species coexisted with C. rhotheus. These shallow areas may have provided more cover, enabling C. perplexus to avoid C. rhotheus. Cottus perplexus did not prefer shallow areas in spring, when increased food abundance apparently eased competition.

In all areas and during all seasons, neither C. rhotheus nor C. beldingi demonstrated any clear preferences for certain distances from the bank (Figs. 14, 15, 16). An examination of the pattern in C. perplexus, however, lends further support to the hypothesis that

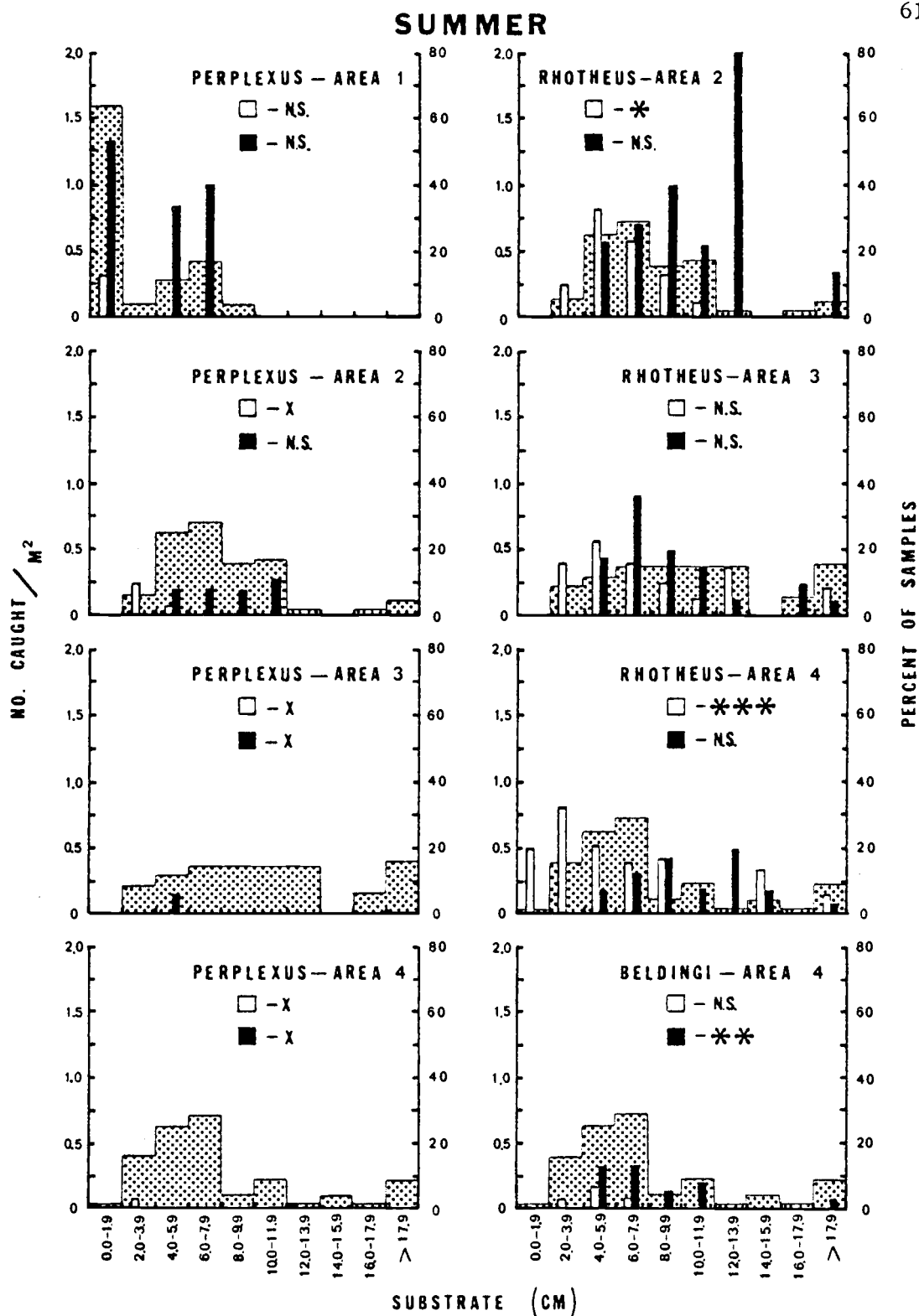


Figure 8. Numerical densities of *Cottus* in summer in relation to mean substrate particle size in riffles. For explanation see legend of Figure 5.

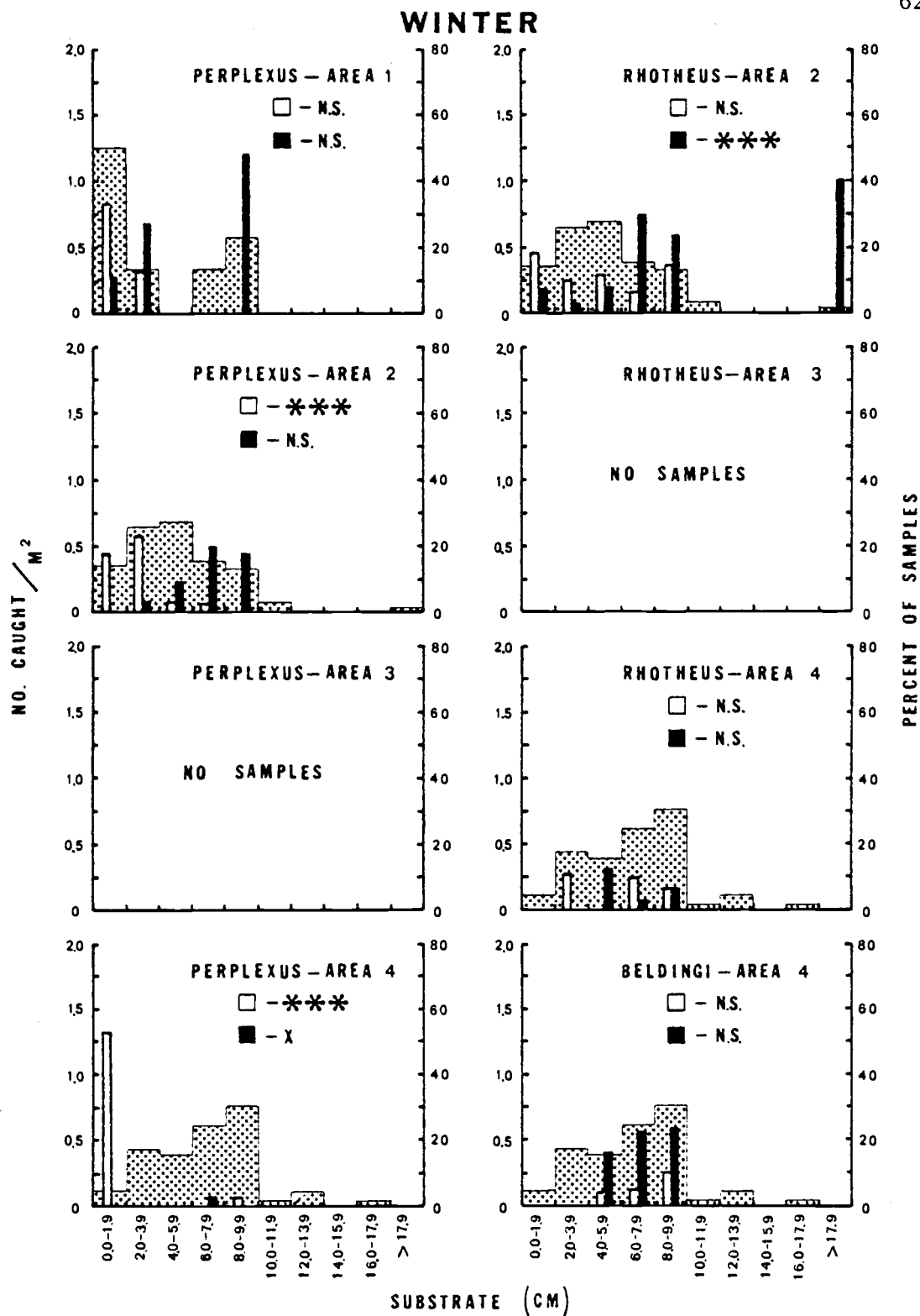


Figure 9. Numerical densities of *Cottus* in winter in relation to mean substrate particle size in riffles. For explanation see legend of Figure 5.

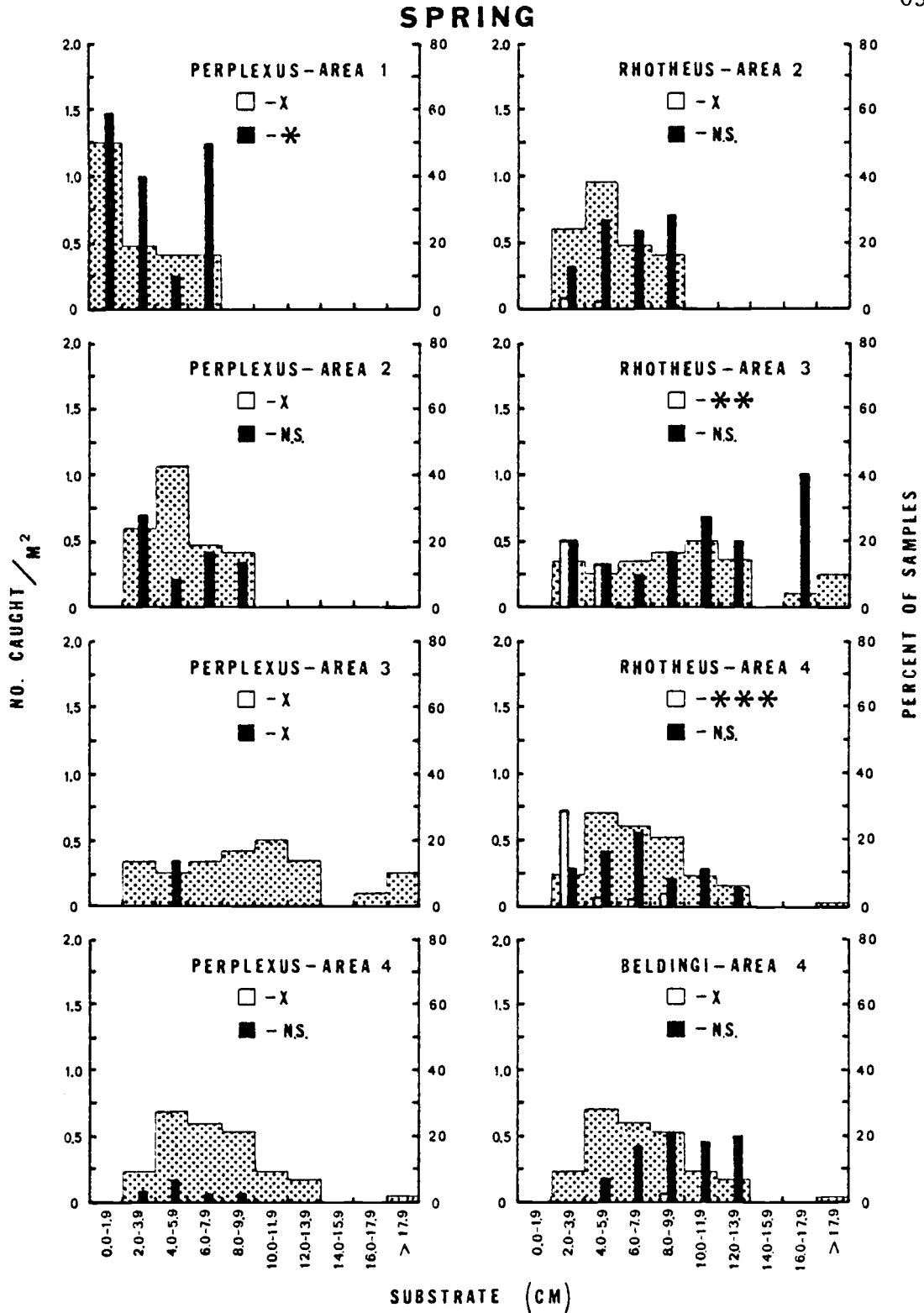


Figure 10. Numerical densities of *Cottus* in spring in relation to mean substrate particle size in riffles. For explanation see legend of Figure 5.

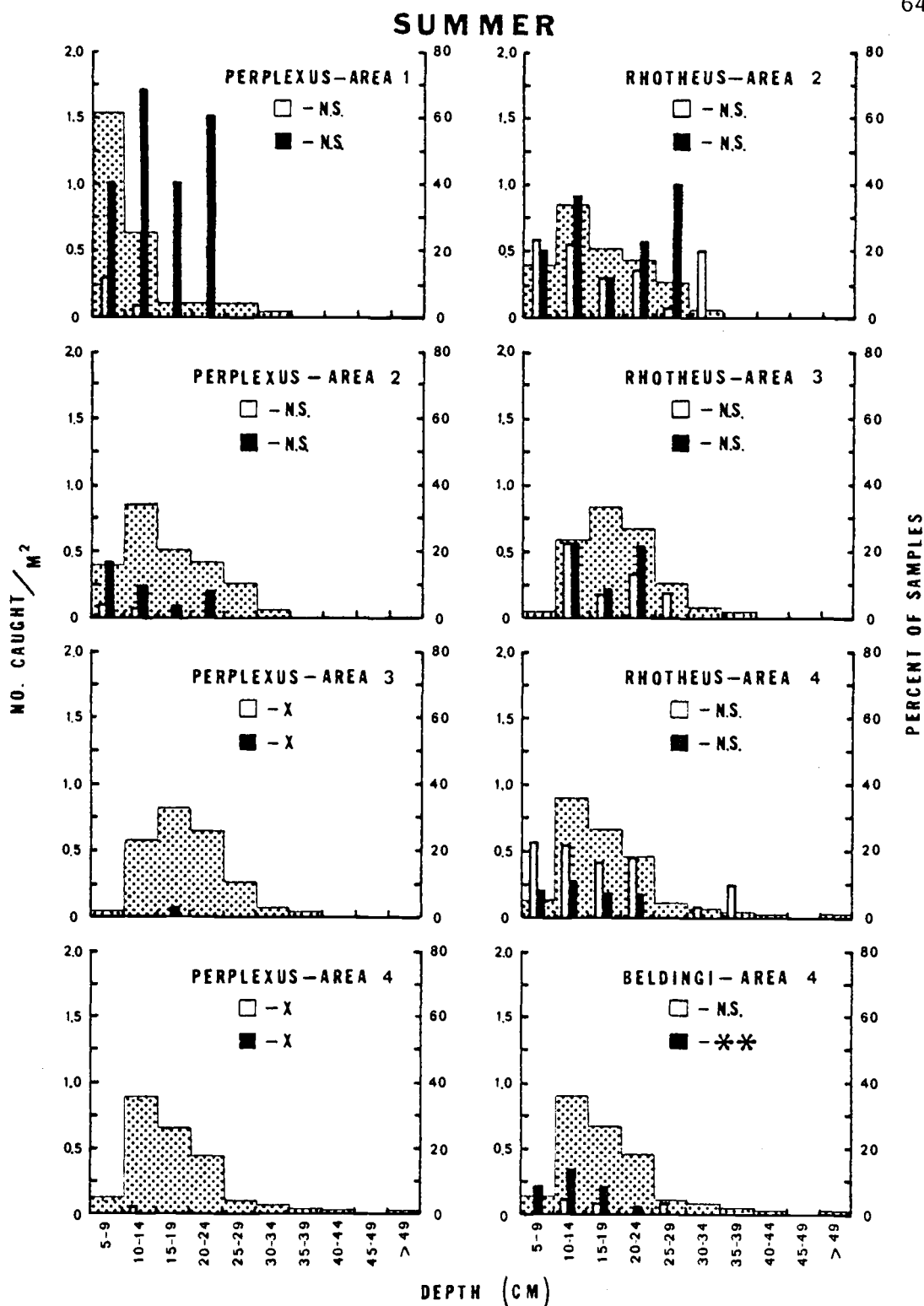


Figure 11. Numerical densities of *Cottus* in summer in relation to depth in riffles. For explanation see legend of Figure 5.

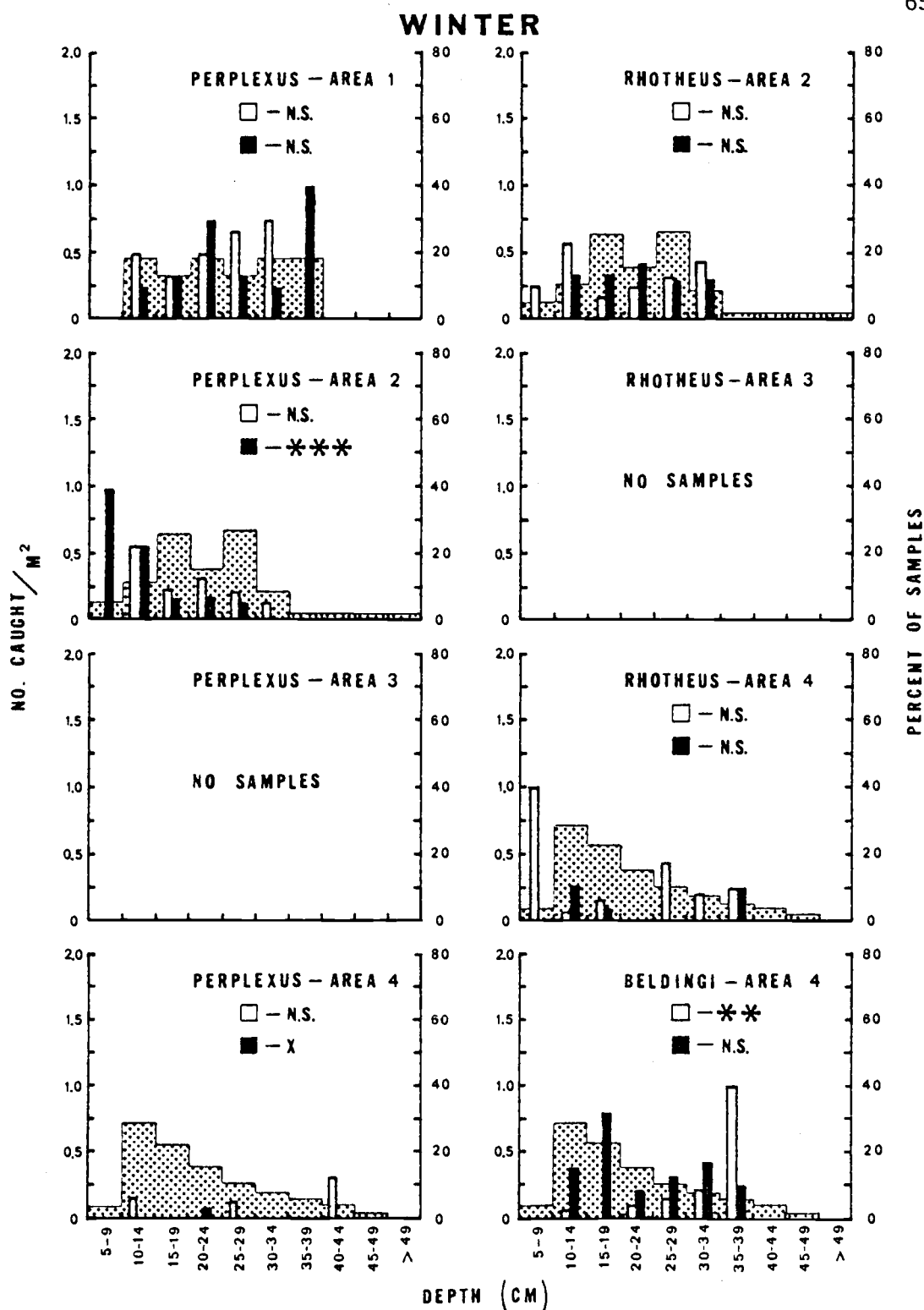


Figure 12. Numerical densities of *Cottus* in winter in relation to depth in riffles. For explanation see legend of Figure 5.

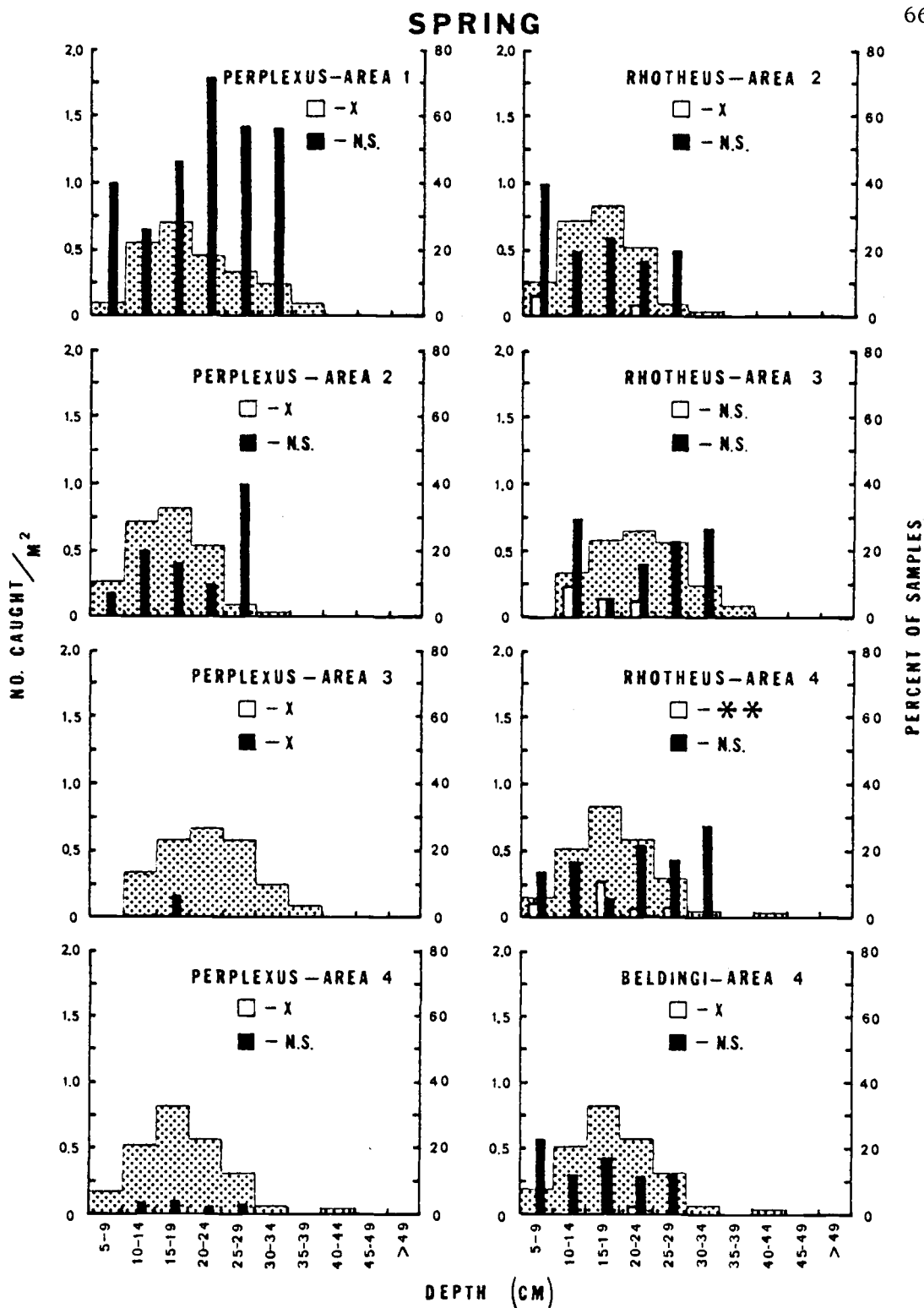


Figure 13. Numerical densities of *Cottus* in spring in relation to depth in riffles. For explanation see legend of Figure 5.

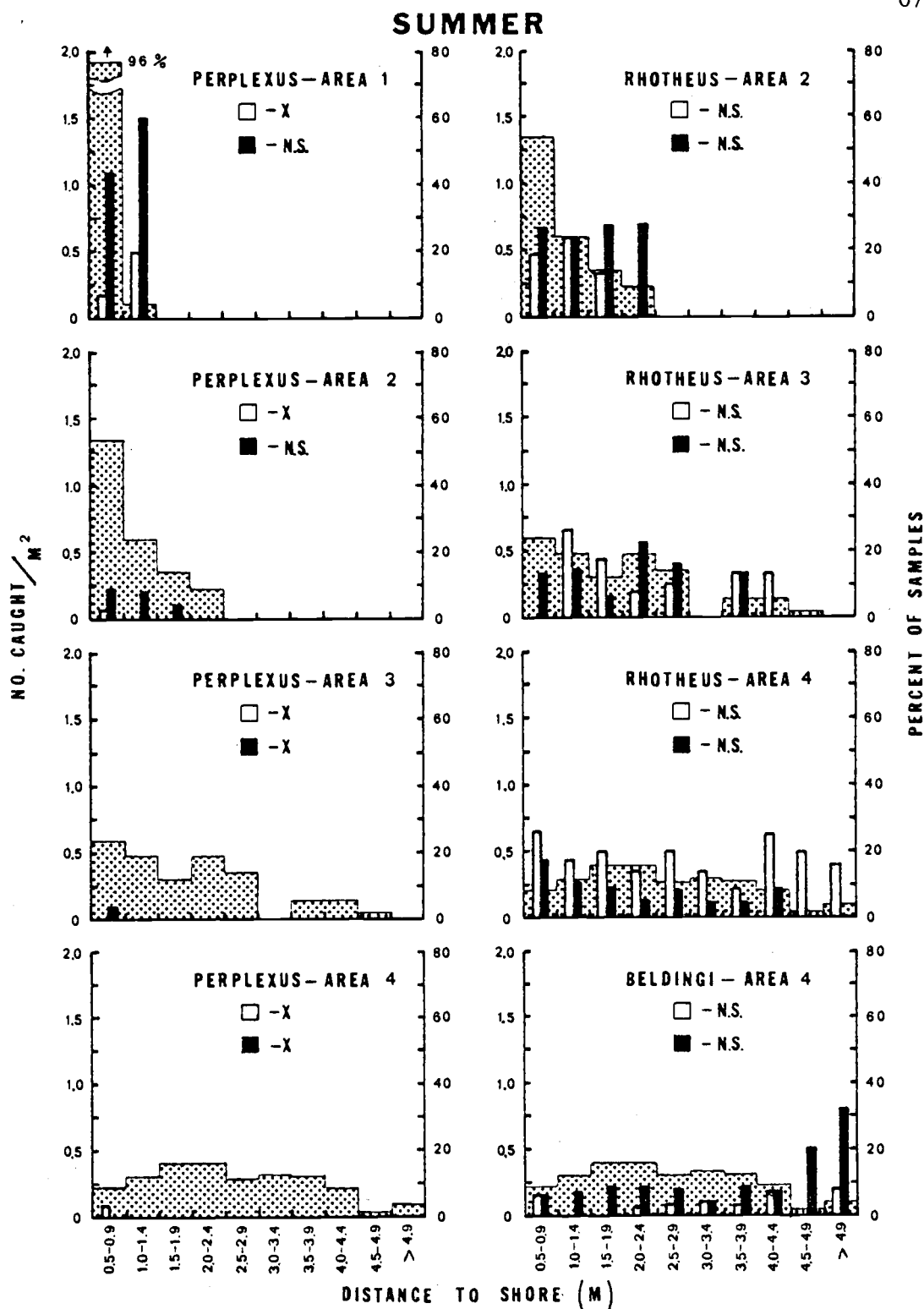


Figure 14. Numerical densities of *Cottus* in summer in relation to distance to shore in riffles. For explanation see legend of Figure 5.

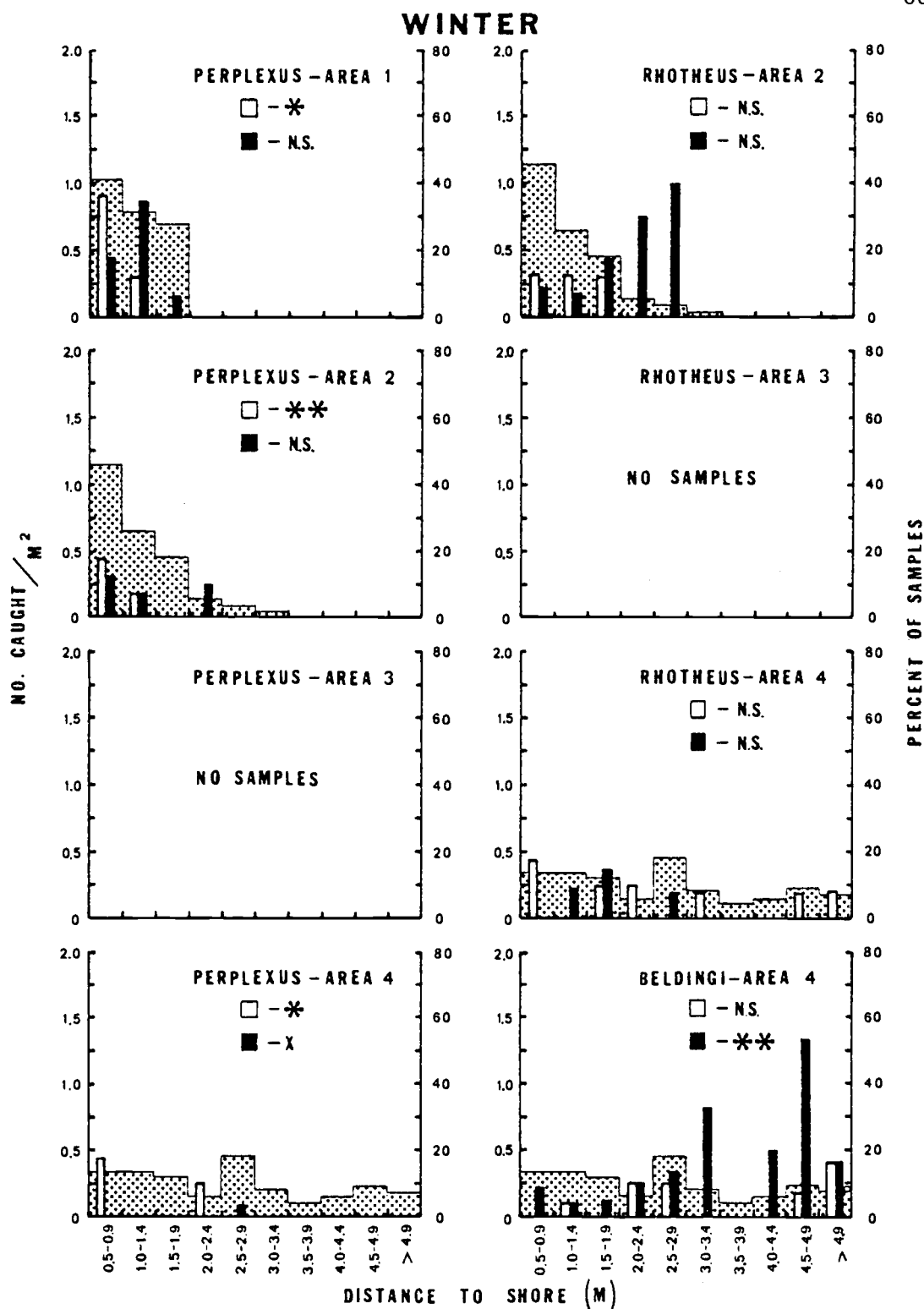


Figure 15. Numerical densities of *Cottus* in winter in relation to distance to shore in riffles. For explanation see legend of Figure 5.

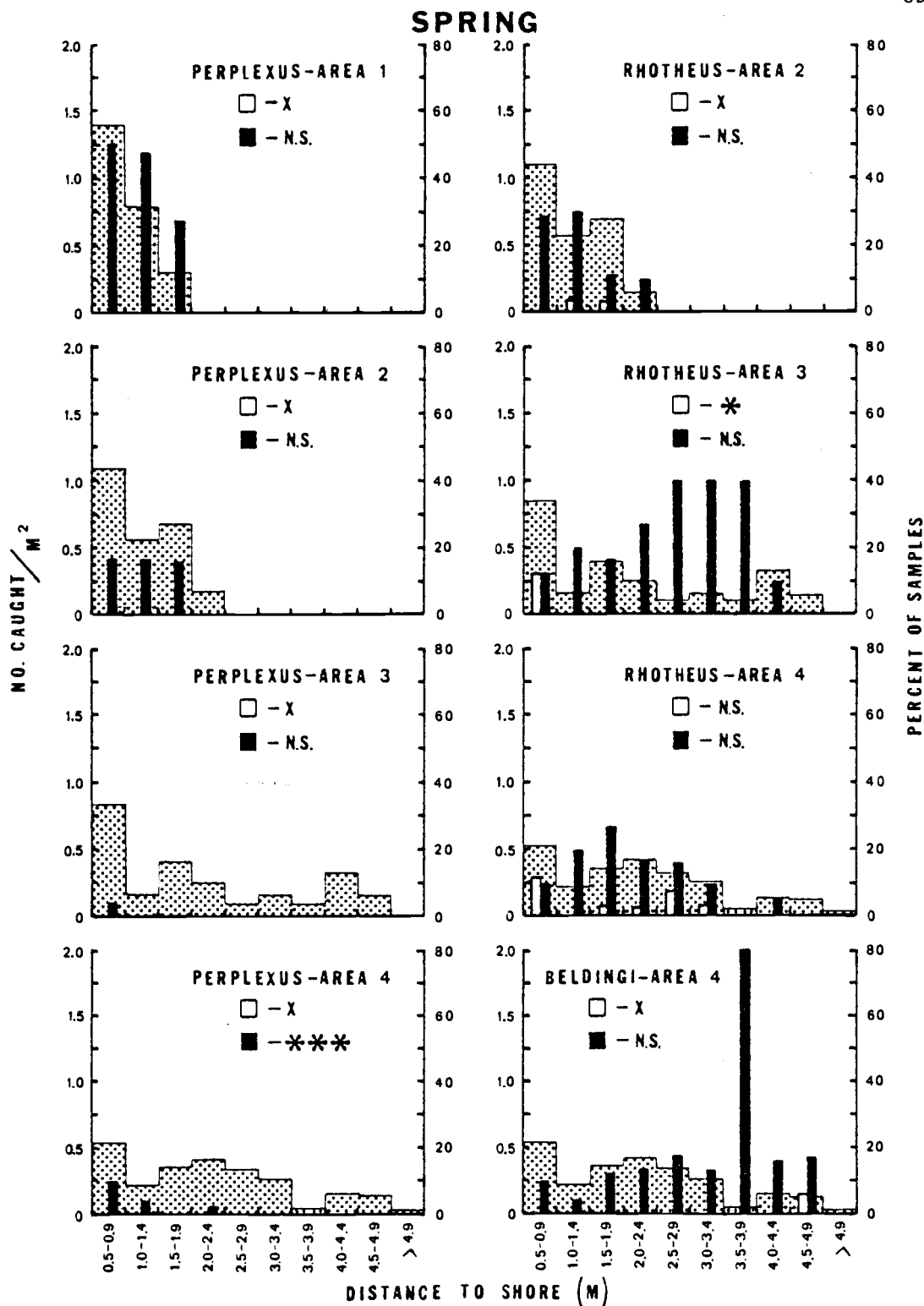


Figure 16. Numerical densities of *Cottus* in spring in relation to distance to shore in riffles. For explanation see legend of Figure 5.

C. perplexus was subject to competition and a small amount of predation by C. rhotheus in Area 2, and competition plus a greater amount of predation by C. rhotheus in Areas 3 and 4. Although C. perplexus used all distances from shore in Area 1, in summer and winter it tended to utilize only the inshore portions of the streams in Areas 2, 3, and 4. These inshore, shallow areas may have provided added cover, as was previously discussed. In spring, however, when competition apparently was relaxed, C. perplexus was found at greater distances from shore in Area 2, but remained confined near the bank in Areas 3 and 4. As was noted earlier, the increased food abundance in spring apparently eased competition, but was not sufficient to significantly affect the predation exerted by C. rhotheus in Areas 3 and 4. Cottus perplexus was therefore restricted to inshore cover in Areas 3 and 4 even in spring.

The overall patterns of species separations and habitat shifts were therefore most clearly expressed in relation to current velocity. These patterns are summarized by the species overlap values for the univariate distributions of Figures 5 - 16 (Table 5). The distributions in relation to the other environmental variables show moderate to high overlaps with little or no pattern across areas and seasons. The only exceptions were the overlaps involving C. perplexus in Areas 3 and 4, where the nearly total exclusion of C. perplexus from riffles resulted in low overlap values for nearly all environmental variables.

TABLE 5. Within-riffle overlap of univariate distributions of adult numerical densities of Cottus in relation to the four environmental variables, calculated from the equation of Levins (1968) as modified by Pianka (1973). Total overlap was calculated as the product of the individual overlaps after Cody (1974).

Environmental Variable	Season	<u>perplexus-rhotheus</u> overlap			<u>perplexus-beldingi</u> overlap	<u>rhotheus-beldingi</u> overlap
		Area 2	Area 3	Area 4	Area 4	Area 4
Current Velocity	Summer	0.260	0.142	0.000	0.000	0.793
	Winter	0.775	--*	0.000	0.000	0.222
	Spring	0.603	0.574	0.718	0.194	0.285
Substrate	Summer	0.552	0.369	0.000	0.000	0.577
	Winter	0.682	--*	0.176	0.613	0.783
	Spring	0.797	0.219	0.771	0.343	0.741
Depth	Summer	0.680	0.267	0.000	0.000	0.929
	Winter	0.391	--*	0.000	0.190	0.553
	Spring	0.722	0.114	0.569	0.743	0.667
Distance to Shore	Summer	0.814	0.346	0.000	0.000	0.349
	Winter	0.469	--*	0.361	0.194	0.158
	Spring	0.919	0.150	0.458	0.146	0.310
Total Overlap	Summer	0.0795	0.0048	0.0000	0.0000	0.1485
	Winter	0.0970	--*	0.0000	0.0000	0.0152
	Spring	0.3186	0.0021	0.1441	0.0072	0.0437

* Sampling impossible due to high water levels.

The total spatial overlaps between species in each area during each season, calculated as the products of the overlaps for the individual environmental variables, further summarize and support the previously discussed patterns (Table 5). Total overlap between C. perplexus and C. rhotheus was generally lowest in summer, when competition apparently was strongest, and highest in spring, when competition was relaxed. This seasonal pattern was, however, pronounced only in Area 2, where predation by C. rhotheus was not as severe as in Areas 3 and 4. Further, in all seasons the overlap between C. perplexus and C. rhotheus was considerably greater in Area 2 than either of the downstream areas, thus indicating that the added predation in Areas 3 and 4 was an important mechanism in excluding C. perplexus from riffles. The total overlap between C. rhotheus and C. beldingi was greatest in summer and lowest in winter. The high overlap in summer is deceiving, however, because the depth to which C. beldingi burrowed into the substrate was not considered as an environmental variable. In winter, the greater current velocity tolerance of C. beldingi enabled this species to remain in areas that C. rhotheus was forced to vacate. This resulted in low overlap between the species and allowed C. beldingi to emerge from the gravel.

May (1975) noted that this calculation of total overlap as the product of the individual univariate overlaps does not take into account that the environmental variables may be interrelated and that the species may react to the environmental variables in combination.

Although in this case current velocity, substrate, depth, and distance to shore were not significantly correlated (Table 6), the reactions of the species to all the environmental variables simultaneously were examined with a multivariate principal components analysis of the environmental data. This analysis also served as a means of evaluating the suitability of calculating total overlap as a product of the individual univariate overlaps.

The principal components analysis, calculated from all 750 riffle samples, generally confirmed the previously discussed findings of the univariate analysis. The first component was highly correlated with all environmental variables; the second component primarily contrasted current velocity and depth. Collectively, these components accounted for 62.25% of the total variability in the data (Table 7). The samples for each area in each season were plotted separately in a two-dimensional space delineated by the first two components; species distributions were then superimposed on the plots (Figs. 17, 18, 19). Cottus perplexus utilized most of the available habitat in Area 1, although areas of rapid current velocity were avoided in winter. The distribution of this species was, however, generally more restricted in Areas 3 and 4. Cottus rhotheus occurred over a wide range of environmental variables, but did avoid the areas of very rapid current velocities. Cottus beldingi was restricted to the shallower portions of riffles with rapid current velocities. Overlap between C. perplexus and C. rhotheus was greater in Area 2 than in Areas 3 and 4; overlap between these species

TABLE 6. Correlations between the environmental variables in riffles. Data from all areas and seasons combined.

Environmental Variable	Current Velocity	Substrate	Depth	Distance to Shore
Current Velocity	1.000	0.066	-0.013	0.219
Substrate	-	1.000	0.186	0.197
Depth	-	-	1.000	0.197
Distance to Shore	-	-	-	1.000

TABLE 7. Correlations between the principal components and the original environmental variables, eigenvalues, and the percent variability associated with each principal component of the environmental data.

Environmental Variable	PC 1	PC 2	PC 3	PC 4
Current Velocity	0.4364	0.7854	0.0243	0.4383
Substrate	0.6244	-0.2800	-0.7257	0.0714
Depth	0.5699	-0.5531	0.4836	0.3680
Distance to Shore	0.7373	0.1997	0.2263	-0.6043
eigenvalue	1.4488	1.0410	0.8124	0.6978
% variability	36.22	26.03	20.31	17.44
cumulative % variability	36.22	62.25	82.56	100.00

SUMMER

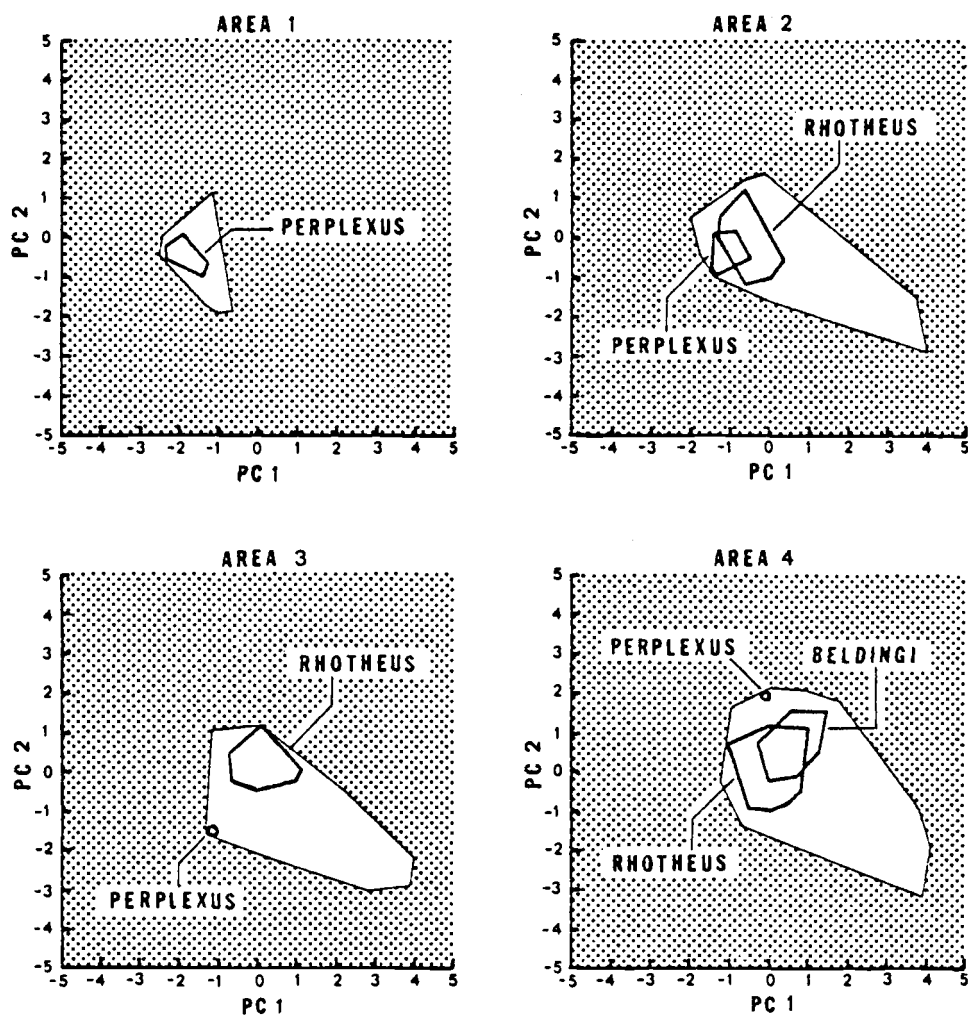


Figure 17. Within-riffle distribution of *Cottus* in summer plotted in relation to the first two principal components of the environmental data. Unshaded area represents available habitat. Polygons contain at least 75% of the individuals of each species.

WINTER

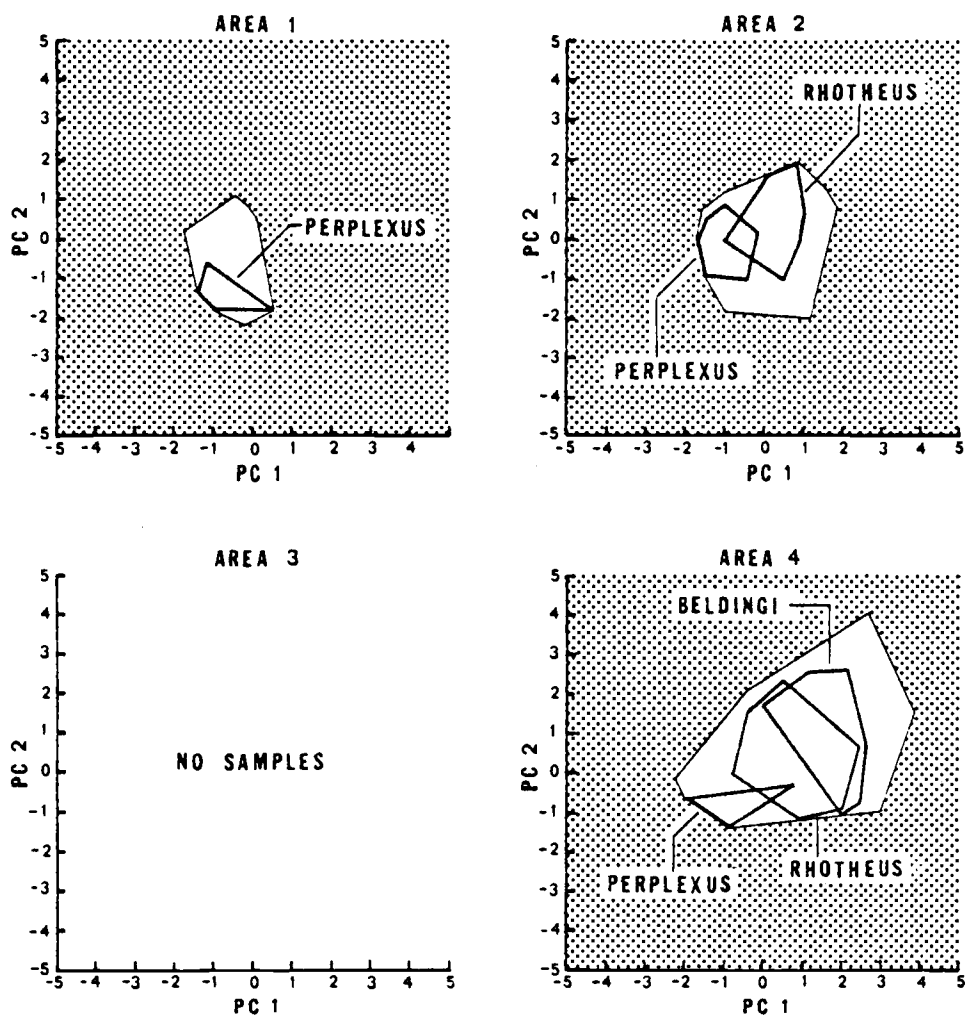


Figure 18. Within-riffle distribution of *Cottus* in winter plotted in relation to the first two principal components of the environmental data. Unshaded area represents available habitat. Polygons contain at least 75% of the individuals of each species.

SPRING

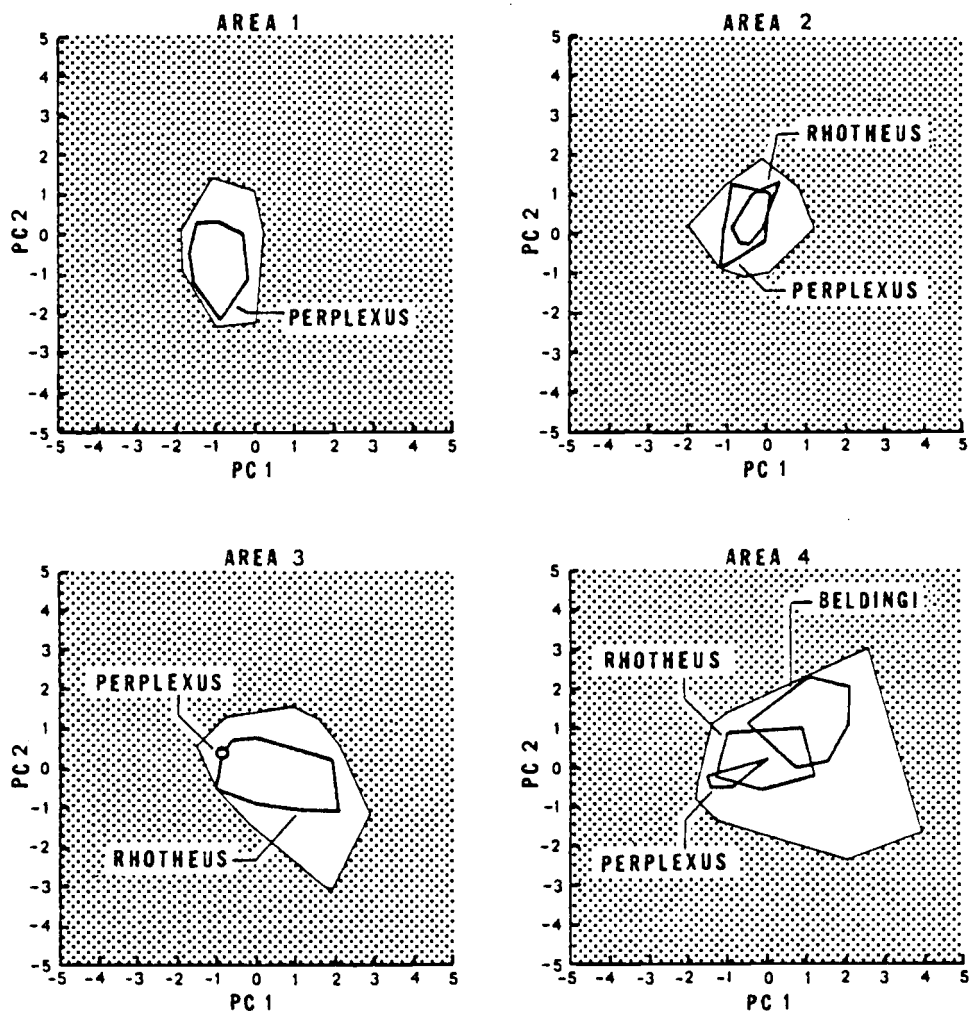


Figure 19. Within-riffle distribution of *Cottus* in spring plotted in relation to the first two principal components of the environmental data. Unshaded area represents available habitat. Polygons contain at least 75% of the individuals of each species.

in all areas was also greater in spring than in summer and winter. Overlap between C. rhotheus and C. beldingi was greatest in summer and lower in winter and spring. As these findings are in agreement with those of the univariate analysis, the data suggest that the simpler, but less mathematically rigorous univariate calculations were appropriate, at least for these species in this environment, where the environmental variables were not strongly correlated.

The three species of Cottus therefore demonstrated clear patterns of habitat utilization that appeared to be related strongly to the presence or absence of other species. Cottus rhotheus apparently was able to exclude C. perplexus partially from riffles and force C. beldingi to burrow into the substrate. The primary basis for this conclusion was the pattern of habitat shifts across areas and/or seasons. The range and distribution of physical environmental variables did, however, vary among areas and seasons. The possibility therefore remained that the changes in use of habitat were related solely to changes in the physical environment and not to the presence or absence of the other species. Further, although both predation and competition appeared to be the mechanisms causing the habitat shifts, the type of competition involved (i.e., interference or exploitation) could not be determined from the field data. These aspects of the problem were examined in the artificial stream experiments.

Artificial Stream Experiments

The sequential addition of the species to the constant environment provided by the artificial streams gave further support for the hypothesis that the use of habitat was related to species interactions and suggested that the competition contributing to the habitat shifts was interference competition for space (Figs. 20, 21, 22; Appendix V). Cottus perplexus, when present in the streams alone, preferred the riffle areas of fast currents, coarse substrates, and shallow depths. Qualitative observations during this period indicated that within the first day after initial introduction, individuals generally found a small cavity in the substrate and thereafter remained in the same location. That individuals were not found in the pools during this period was definitely not related to catchability; the fine sand substrate in the pools made observations and capture much easier there than in the riffles dominated by cobble-sized rock substrates.

The introduction of C. beldingi into the streams resulted in the shift of C. perplexus to areas of slower currents, slightly finer substrates, and greater depths. Cottus beldingi, as in the field, preferred the fast-flowing, shallow riffles with cobble substrates. Apparently C. beldingi was more efficient than C. perplexus in using these areas and was able to force C. perplexus into the other portions of the streams. Several of the cavities in the substrate originally occupied by C. perplexus were noted to be used later by C. beldingi. Although the limited experimental design did not allow the

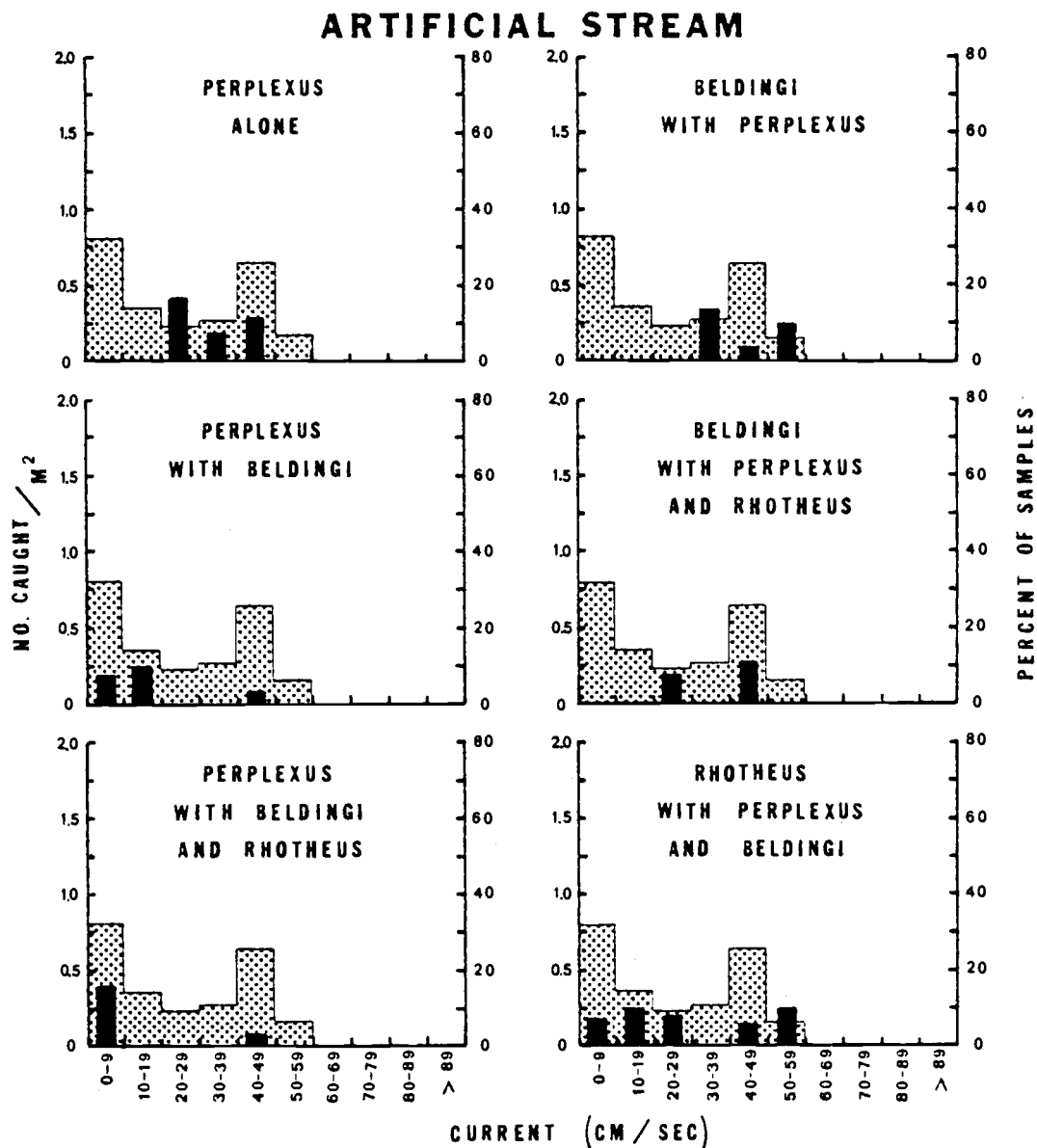


Figure 20. Numerical densities of *Cottus* in each species combination in relation to current velocity in the artificial streams. Black bars represent numerical densities; values are read from the left axis. Stippled area represents the distribution of samples; values are read from the right axis.

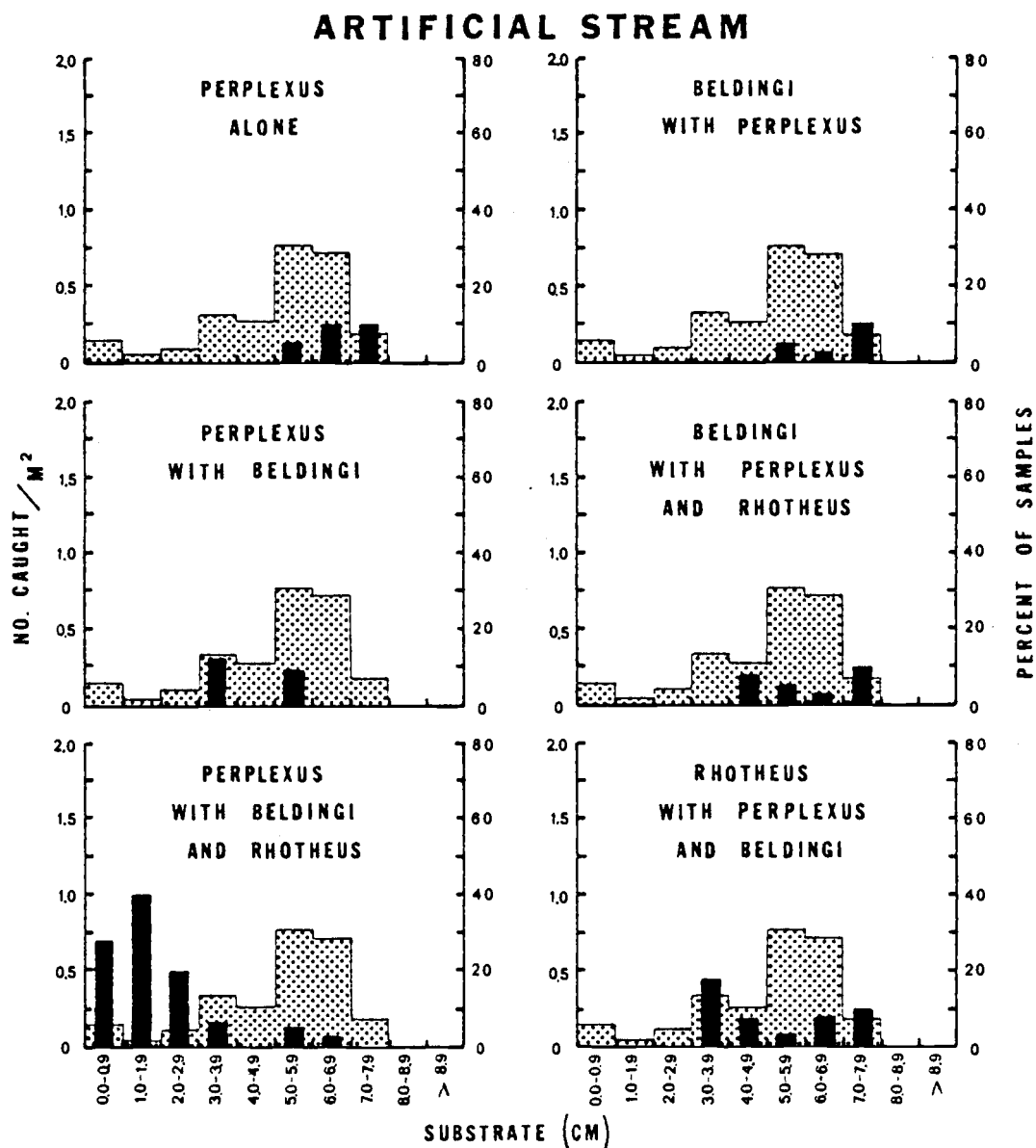


Figure 21. Numerical densities of *Cottus* in each species combination in relation to mean substrate particle size in the artificial streams. Black bars represent numerical densities; values are read from the left axis. Stippled area represents the distribution of samples; values are read from the right axis.

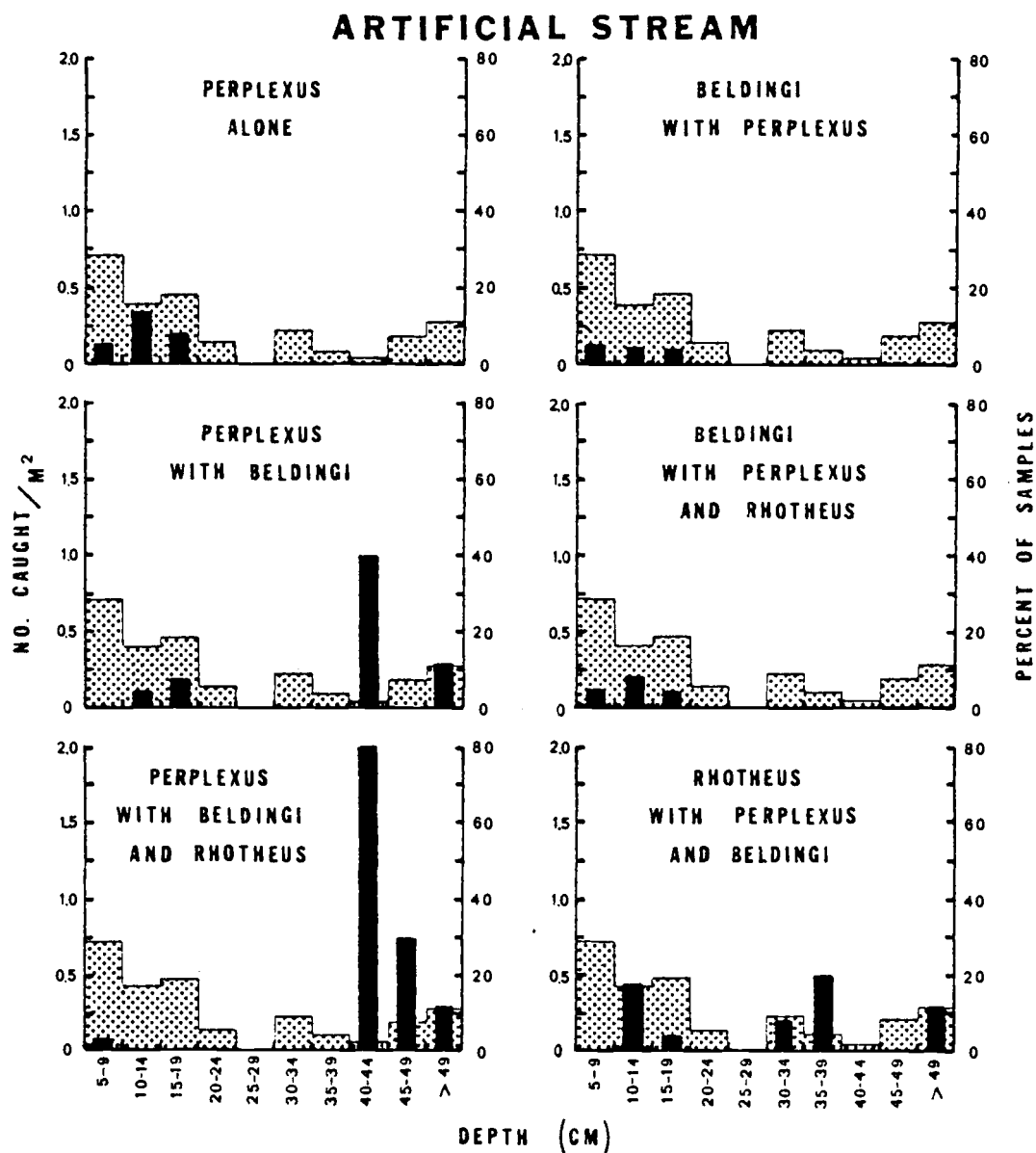


Figure 22. Numerical densities of Cottus in each species combination in relation to depth in the artificial streams. Black bars represent numerical densities; values are read from the left axis. Stippled area represents the distribution of samples; values are read from the right axis.

establishment of a control to determine whether this shift by C. perplexus was merely the result of its having spent more time in the streams than C. beldingi, this alternative appears very unlikely. Daily qualitative observations indicated that the shift by C. perplexus occurred quite rapidly, within 24 hrs after the introduction of C. beldingi. The rapidity of this habitat shift also suggested that the mechanism involved was interference competition for space. The C. perplexus and C. beldingi used were all of approximately the same size (Appendix V), hence predation between these species could not have occurred. Similarly, a shift due to exploitation competition would not be expected to occur in such a short period of time (Miller 1969).

The addition of C. rhotheus into the streams created a pattern of habitat utilization very similar to that encountered in the field. With the added competition and predation by C. rhotheus, C. perplexus was confined even more rigidly to the pools than it had been when coexisting only with C. beldingi. The distribution of C. beldingi was not drastically affected by the addition of C. rhotheus. Apparently, as in the field in summer, C. beldingi was able to avoid C. rhotheus by utilizing the interstitial spaces of the cobble substrate. Cottus rhotheus was found in nearly all areas of the streams. It therefore utilized pools in the artificial streams to a greater extent than it usually did in the field. The food available in the artificial streams consisted of the insect fauna that had been able to colonize the substrate; the density of food was rather sparse

when compared to most actual stream environments. The artificial streams may therefore have modeled the field situation in late summer. At this time of food scarcity C. rhotheus was captured in high density in the pools of the small streams of Area 2. In the small artificial streams, C. rhotheus may similarly have wandered into the pools in search of prey. Qualitative observations indicated that C. rhotheus usually moved actively through the pools for short periods of time before returning to the riffles.

DISCUSSION

The three species of Cottus in the Marys River segregate in an orderly manner in space and this segregation apparently is due at least in part to species interactions. The integration of these results with considerations of resource availability patterns and the abilities of the species to exploit these resources efficiently suggests several generalities about the mechanisms producing structure in freshwater fish communities and the evolutionary patterns of Cottus in western North America.

General Patterns of Segregation in Freshwater Fishes

The three species of Cottus studied in this thesis were shown to segregate in space, and the natural history literature reviewed above indicated that nearly all species of Cottus appear to have similar food habits and temporal activity patterns. Habitat is apparently the most important variable upon which interactive segregation in this sculpin guild is based. The question therefore arises as to whether this is a general tendency in freshwater fishes.

Schoener (1974), in his review of the evidence of segregation in a wide variety of communities, noted that habitat was much more commonly divided among species in the same community than was either food or time. The empirical results compiled by Schoener were therefore in general agreement with the niche compression hypothesis of MacArthur and Pianka (1966) and MacArthur and Wilson (1967), which

predicted that as species are added to a community, each species should restrict its use of habitat but not significantly change its diet. These observations of segregation and the outpouring of species packing theory that followed (e.g., see review by Pianka 1976) were, however, primarily directed at terrestrial vertebrate communities.

The different life history patterns of fishes and the peculiarities of freshwater environments invalidate most theoretical treatments and make the extension of terrestrial generalities to the aquatic environment tentative at best. Keast (1977) and Werner (1977) have noted that unlike birds or mammals, fishes do not undergo well-defined deterministic growth. Whereas in most homeotherms an individual reaches adulthood relatively quickly and retains similar ecological habits for the remainder of its life, in fishes many characteristics may continue to change dramatically with increasing age and size. The populations of most fish species therefore usually contain a wide variety of different size groups with different ecological habits.

The freshwater environment is also fundamentally different from the terrestrial in that available food is often concentrated in space and extremely variable in time. This is particularly true of temperate streams, where aquatic insect larvae and small fishes, the principal food of most stream fishes, are usually found in greatest density in limited portions of the habitat and are available only during certain times of the day and year (e.g., see Hynes 1970).

In lakes and in tropical aquatic environments, where fishes appear to feed on a wider variety of prey, this pattern is also prevalent to some extent, but is probably not as pronounced due to the greater diversity of prey and the relative constancy of the environment (e.g., see Hutchinson 1967; Lowe-McConnell 1975).

Consideration of these differences indicates that in fish communities, like their terrestrial counterparts, species should segregate with regard to habitat more frequently than with regard to food habits or temporal activity patterns. This result is predicted, however, for different reasons than those postulated for terrestrial communities. This general pattern is also more likely to be followed in temperate streams than in lakes or in the tropics. In most fish populations specialization on any niche axis should be difficult due to the many different size classes present. The changes in ecological habits with increasing age and size are, however, generally least pronounced with regard to the use of habitat. Although in many species the predation-prone youngest age class remains in dense cover or shallow inshore areas and is thus separated from the older individuals, there is generally little intraspecific habitat segregation among the remaining age classes (e.g., see Werner et al. 1977). Food use, however, often changes dramatically throughout life and makes food specialization for a species difficult (Schoener 1974; Werner 1977). Interspecific food-based segregation will be unlikely in these species. With each age class feeding on different items, trophic levels will tend to lose their

distinctiveness and species interactions may occur through complex combinations of predation and competition among the different size classes of each species. Species segregation based on food habits would therefore be possible only for species that were very different morphologically and, as a result, fed on very different items for their entire life spans.

The temporal variability in food availability further reinforces the low probability of segregation based on food and also makes temporal segregation unlikely. A fish species that was very plastic in its food habits and temporal activity patterns would be best suited to take advantage of the fluctuating food supply opportunistically (Larkin 1956). Food items are, however, generally in greatest density in a limited area in the environment, as noted above. Most species would therefore be expected to be generalists with regard to food and time, but to prefer the areas of space with the greatest food supply. Species segregation would therefore be difficult if based on food or time, but much more likely if based on habitat, because the areas with the greatest food supply remain relatively constant through time and nearly all age classes of most species have similar patterns of habitat utilization. This inability to divide food and time should, however, be more prevalent in temperate streams than in lakes or tropical freshwater environments, where the temporal variability in food availability is apparently less pronounced.

Although there are relatively few data available on the patterns of segregation in freshwater fish communities, those which are available tend to support this hypothesis. Lagler (1944) and Larkin (1956) noted that most fishes in temperate fresh waters are food generalists. Although food habits studies frequently demonstrate differences in the type of food taken by coexisting species, the differences are often the result of the species using dissimilar portions of the environment rather than due to any active selection of a narrow range of prey types (Johannes and Larkin 1961; Werner 1977; Werner et al. 1977). In his reviews of interactive segregation in fishes, Nilsson (1967, 1978) noted that habitat was the most commonly divided environmental variable. The exceptions to this general rule were those predicted above; i.e., species that were very different morphologically or species from lakes or tropical environments. Werner (1977) noted that the largemouth bass (Micropterus salmoides) and the bluegill (Lepomis macrochirus) did not segregate in space but demonstrated very little overlap in food. These species are, however, very different morphologically. The bluegill has a small, protrusible mouth and feeds on plankton extensively, while the wide gape of the bass allows it to be nearly totally piscivorous even early in life. These species are also lake dwelling, as are the whitefishes (Coregonus spp.), which Nilsson (1967) noted do partition food. Zaret and Rand (1971), Fryer and Iles (1972), and Lowe-McConnell (1975) have given many examples of segregation in tropical freshwater species. Although habitat is

commonly divided, there are many instances of segregation based on food and time. That the nature of lentic and tropical freshwater environments allows segregation on more niche dimensions than are possible in temperate streams may be the primary reason why these environments generally contain more diverse fish faunas.

These relations may also have a bearing on the patterns of longitudinal succession in lotic fishes. Hynes (1970) and Hawkes (1975) have reviewed much evidence which indicates that the number of fish species present generally increases with increasing distance from the headwaters of a river system. As was observed for the Cottus species in this study, the pattern is often one of species additions downstream rather than sequential longitudinal replacement (Horwitz 1978). Harrel et al. (1967), Sheldon (1968b), Whiteside and McNatt (1972), and Lotrich (1973) have quantified the relation and speculated that this was at least in part due to increased spatial heterogeneity downstream. Species diversity could therefore be greater downstream due to more opportunities for habitat segregation; Finger (1974) and Gorman and Karr (1978) have quantitatively demonstrated that fish species diversity in rivers is often correlated with habitat diversity. The lower reaches of river systems, however, also offer a wider variety of prey types and exhibit less environmental fluctuation than small streams (Horwitz 1978). Thus, as was discussed above for lakes and tropical freshwater environments, the lower reaches of river systems may support diverse fish faunas because they also offer more opportunities for segregation on the food and time axes of the

niche.

Mechanisms of Segregation in Stream Fishes

The above theoretical treatment and supporting empirical evidence indicate that habitat is potentially the most easily divided environmental variable in streams and is therefore the most frequent basis for interactive segregation in temperate stream fishes. The interactive mechanisms involved in this segregation, however, have not yet been specifically considered. To evaluate the relative importance of these mechanisms requires consideration of which resources are partitionable and which are limiting, the pattern of resource variability in time and space, and the efficiencies of the species in utilizing the resources.

Food is often assumed to be the resource limiting the overall density of fishes (e.g., Weatherley 1972). Although this assumption is quite speculative for this study, there is some evidence that food may be the factor limiting sculpin abundance in the Marys River. Total sculpin biomass was generally low in the riffles of Areas 1 and 3 and in the pools of all areas. In Area 3, riffles were dominated by large rocks imbedded in fine substrate material; this area appeared to support fewer aquatic insect larvae, the principal food of Cottus, than did the areas with riffles containing primarily loose, cobble-sized rocks. Similarly, the dominant fine substrate in the riffles of Area 1 also appeared to support low densities of insects. Hynes (1970) has also noted that pools are generally depauperate in insect

biomass. In my study the greatest densities of sculpins were thus found in the areas with the greatest amount of food. Further, in late summer when food supplies were apparently at their lowest levels, many sculpins, particularly those of Area 1, were observed to be in an emaciated condition, thus suggesting that the paucity of food during this period may be the factor limiting sculpin biomass.

The ability of the species to exploit a limiting resource during times of resource scarcity can be expected to be of critical importance in producing community structure. Although food may often be limiting, food-based segregation by stream fishes is, however, not readily possible, as was discussed above. The more commonly observed habitat segregation may therefore be an indirect means by which the limiting food supply is divided among species. Miller (1969) has noted that when compared to direct exploitation competition for the limiting resource, interference competition "is a more highly evolved strategy in which some form of space is substituted for a resource and is the proximate object of competition." Magnuson (1962) has offered experimental evidence that this pattern can occur within a population of Oryzias. This pattern of species interaction is also suggested when field observations indicate that the spatial segregation of coexisting species is less strict during periods of food abundance than during periods of food scarcity. In this study, C. perplexus and C. rhotheus exhibited increased spatial overlap in Area 2 in spring when food was most abundant. Nilsson (1960, 1963, 1965), Gee and Northcote (1963), and Keast (1965) observed similar

patterns in other fishes.

In addition to being generally difficult to partition, food in streams is also not uniformly distributed in space. The density of aquatic insect larvae is generally much greater in riffles than in pools (Hynes 1970). Sedentary, benthic fishes like sculpins, which feed primarily on these insects, can be expected to prefer to exist in riffles, where the food supply is greatest. The ability to realize this preference, however, must be considered with regard to the comparable preferences of similar, coexisting species. Due to the advantages in foraging efficiency associated with existing in the areas of the greatest food supply, some species appear to have evolved to become highly efficient at utilizing the choice areas of the environment. Such efficiency would entail morphological and physiological adaptations that allow persistence in the physical environment present and the ability to utilize the resource in the presence of other species, either by exclusion through dominance or by avoidance through extreme specialization. The specializations of these species, however, generally result in the loss of the capacity to persist over a wide range of environmental conditions. Other, more generalized species, although less efficient at utilizing the choice areas of the environment, may have retained more flexibility and are able to persist either by being able to colonize areas biogeographically inaccessible to the specialized species or by occupying marginal areas of the environment in the presence of the specialists.

Specialists can be expected to be present only in the most favorable portions of the environments they have been able to colonize, but due to their specializations, will have more restricted distributions than generalists. In environments that specialized species have not been able to colonize, generalists can be expected to occupy a wide range of conditions. The more favorable areas of these environments will be preferred, but intraspecific competition will act to expand their range of existence. In the presence of specialized species, however, the generalists will undergo a shift in their use of habitat and will be found only in the marginal portions of the environment. This pattern will therefore result in the asymmetrical niche shifts predicted from theory by Roughgarden (1972) and Wilson (1975) and demonstrated in fishes by Nilsson (1960, 1963), Andrusak and Northcote (1971), Schutz and Northcote (1972), and Werner and Hall (1976).

In addition to the interference competition by which specialized species are able to exclude other species from the choice areas of the environment, predation can also be expected to play a role in many instances. In fishes, the relative importance of these mechanisms is determined by the size structures of the respective populations. In many guilds, including those composed of species of Cottus, the wide range of size classes present in each species can result in complex combinations of interference competition and predation. For example, from the results of this study, C. rhotheus and C. beldingi appear to be specialists, while C. perplexus is apparently a

generalist. In Area 2, where the population of C. rhotheus contained few large individuals, this species was able to exclude C. perplexus partially from riffles, primarily through interference competition, as previously discussed. In Areas 3 and 4, however, where more large C. rhotheus were present, C. perplexus was nearly totally excluded from riffles by the additional strong predation. Although C. beldingi and C. perplexus never occurred in the field without the presence of the dominant C. rhotheus, in the artificial streams C. beldingi was able to exclude comparably sized adult C. perplexus partially from riffles solely through interference competition for space. Within this type of guild structure competition and predation are thus complementary in their effect on the use of habitat by the species and their relative importance can be expected to vary with the size composition of the populations of the respective species.

A Model of Interactive Segregation in Cottus

A general model of interactive segregation in Cottus is useful to integrate the empirical results of this study with the above discussion and to extend these results to a general, theoretical level useful for the investigation of patterns in other guilds of benthic vertebrates. With regard to the above data and discussion, the model will be based on the following substantive statements:

- (1) The segregation in this Cottus guild is based primarily on habitat and, more specifically, on the variations in current velocity in space, and
- (2) the segregation of the species is affected by their

ability to adapt to the physical environment and their ability to utilize resources in the presence of other, coexisting species. Because the overall ability of the species to use habitat depends on this array of factors, the model will examine an overall measure of the potential ability of each species to utilize the habitat. The ability of each species is thus considered as its potential, and is therefore distinguished from a given performance, or how it actually utilizes the habitat in any specific environment. Potential thus encompasses many possible performances and was deduced for each species by considering the results of this study, the natural history literature on Cottus, and qualitative observations made on these species in other river systems. The model is, however, oriented specifically toward interactive segregation and examines this potential in relation to current velocity, the environmental variable upon which segregation in this guild is most strongly based. Other environmental variables that may affect the longitudinal or geographical distribution of the species (e.g., substrate, temperature) are not considered. To study the effects of these variables would require extension of the model.

The three species in the Marys River then appear as in Figure 23. Cottus perplexus, a generalist species, has peak potential considerably lower than those of the other, specialist species. Cottus perplexus has a slight peak in potential in riffles, as demonstrated by its preferences when in the artificial streams alone, but maintains a similar potential over a wide range of current

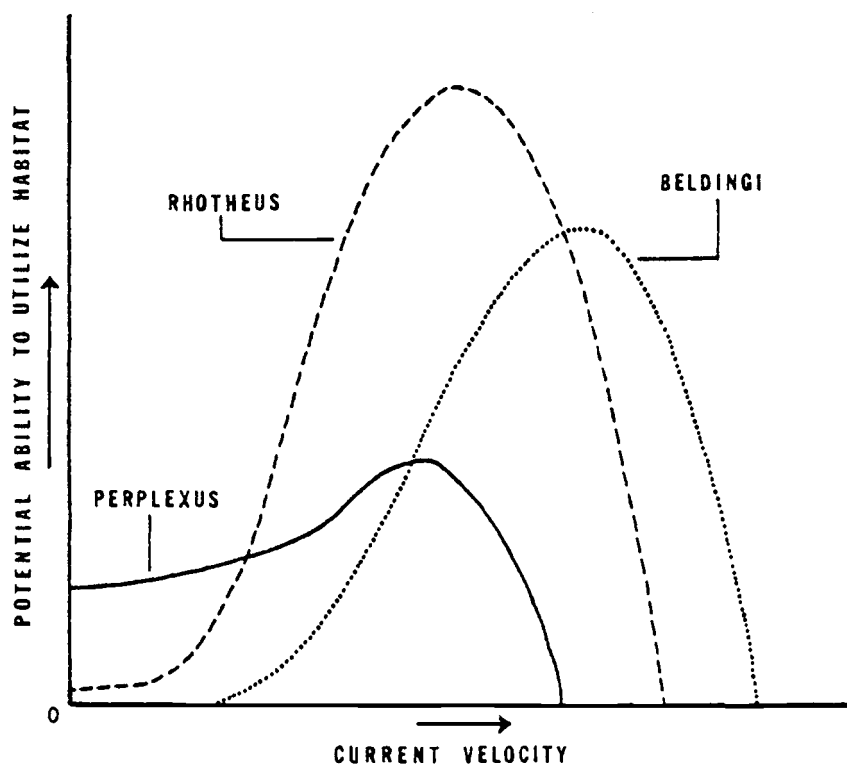


Figure 23. A model of interactive segregation in the Cottus guild in the Marys River. See text for explanation.

velocities that extends into pools. Cottus beldingi was never found in pools in the Marys River or the artificial streams; the potential of the morphological form of this species that exists in the Marys River was therefore assumed to drop to zero for slow current velocities but to remain high in very fast currents. Cottus rhotheus, due to its predation- and competition-based dominance over the other species, maintains the highest potential over a wide range of riffle currents, but its potential drops to zero at lower current velocity ranges than those that mark the upper limit of C. beldingi. Because C. rhotheus was occasionally found in low densities in pools, its potential in very slow current velocities was assumed to be low, but nonzero.

The model can then be used to summarize the patterns of interactive segregation in the Marys River. Cottus perplexus, with its nearly uniform potential over a wide range of current velocities, can exist in many parts of the environment. When it occurs alone in areas that the specialist species have been unable to colonize due to inaccessibility or unsuitable substrate, it will prefer riffles, where it has peak potential. Intraspecific competition, however, will readily force many individuals into pools, where its potential is nearly as great. In areas where C. perplexus coexists with C. rhotheus, C. perplexus can persist only in the slow current velocities, where its potential exceeds that of C. rhotheus. Riffles will be dominated by C. rhotheus, but intraspecific competition will force some individuals of this species into pools, where it has low

potential. The decrease in potential when moving to slow currents is, however, much greater for C. rhotheus than for C. perplexus; greater intraspecific competition will therefore be needed to force C. rhotheus into pools. Thus, while C. perplexus will frequently be found in slow currents, even when it exists alone, C. rhotheus will commonly occur in pools only during periods of extreme food scarcity, as occur in late summer. Where C. beldingi coexists with C. rhotheus, its potential exceeds that of C. rhotheus only in areas with very fast current velocities. In winter and spring it is able to persist by utilizing these areas. During the late summer, however, when food supplies are at their lowest levels, few riffles in the Marys River contain current velocities this rapid. At this time C. beldingi is able to persist only because it is extremely specialized for burrowing and is thus able to utilize a niche dimension not considered in this model. That C. beldingi is not found in Area 3 in the Marys River can be explained in that the dominant, imbedded substrate material in this area does not allow this species to burrow and thus prevents the exploitation of the added niche dimension required for coexistence.

This model thus relates the similarities of the species and the range of current velocities available in a given locale to the number of niche dimensions required for coexistence. If the major basis for segregation in other lotic sculpin guilds is also current velocity, as appears to be the case in those that have been studied, the model can be used to explain their patterns of spatial segregation. For

example, Bond (1963), Ringstad (1974), and Mason and Machidori (1976) noted that Cottus asper and C. aleuticus commonly coexist in the same reaches of many coastal Pacific slope streams. In areas where C. aleuticus occurs alone, it exists in both pools and riffles. In the presence of the large, dominant, and pool dwelling C. asper, however, C. aleuticus is confined to riffles. These species may therefore appear as in Figure 24(a). The large, piscivorous C. asper, which undoubtedly exerts severe predation on C. aleuticus, has a much greater potential ability to utilize the habitat in pools. The two species are able to locally coexist, however, because the potential of C. aleuticus is greater than that of C. asper in the faster currents.

Contrastingly, Bond (1963) noted that although C. beldingi and C. confusus commonly occupy the same river systems, their distributions rarely overlap longitudinally. Cottus confusus commonly occupies cold headwater areas and spring creeks alone, while C. beldingi exists by itself in the lower reaches of the same river systems. Bailey and Bond (1963) noted that these species also appear to be closely related taxonomically. The ecology of C. confusus has not been well studied. Further, the C. beldingi in the Cascade Mountains and other areas where C. confusus occurs appear to be a different morphological form from those in the Marys River (pers. obs.). Their respective potentials in relation to current velocity are therefore unknown, but may appear as in Figure 24 (b and c). Cottus confusus, which appears to be physically adapted to cold streams, may have greater potential

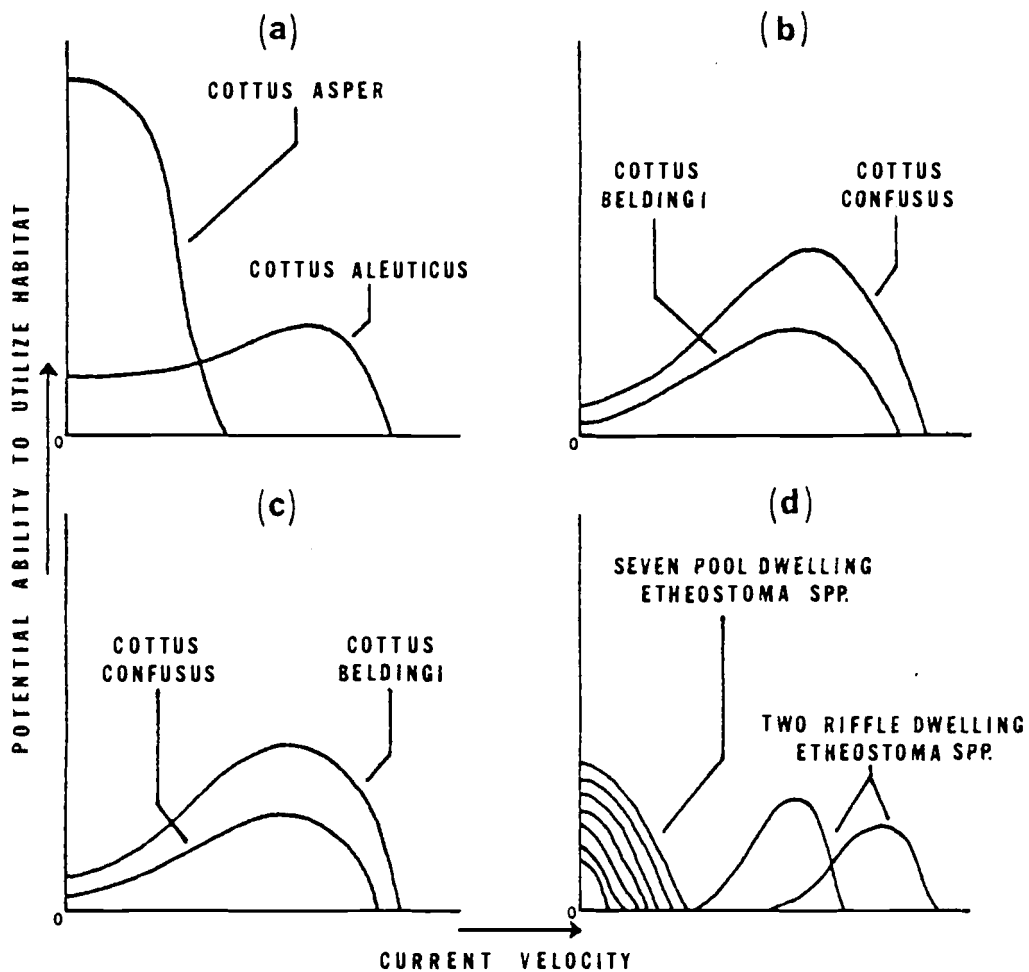


Figure 24. Models of interactive segregation in several guilds of benthic fishes.

- (a) *Cottus asper*, *Cottus aleuticus* in many coastal Pacific slope streams.
 - (b) *Cottus beldingi*, *Cottus confusus* in headwater areas of Cascade streams.
 - (c) *Cottus beldingi*, *Cottus confusus* in downstream areas of Cascade streams.
 - (d) *Etheostoma* spp. in the Cumberland, Tennessee, and Green River systems.
- See text for further explanation.

over the entire range of available current velocities and is thus able to exclude C. beldingi from cold areas (Fig. 24b). In the warmer streams, however, the situation may be reversed (Fig 24c). These figures can therefore be considered as two cross-sections of a three dimensional figure in which the relative height of the potential curves changes in relation to temperature. These species are unable to segregate in relation to current velocity and in these streams are also apparently unable to exploit another niche dimension to allow local coexistence. They are therefore forced to separate longitudinally.

There is some evidence that this pattern of segregation based primarily on current velocity may also be prevalent in guilds of benthic fishes taxonomically unrelated to Cottus. For example, Page and Schemske (1978) noted that seven pool dwelling species of darters (Etheostoma), although present in contiguous river systems, are geographically separated. Two riffle dwelling species of the same genus, however, commonly occupy the same reaches of these river systems. Local coexistence is therefore possible for the riffle species but not for the pool species. These species may appear as in Figure 24(d). Although the riffle species have a wide range of currents upon which to segregate, the pool species all inhabit the same small range of low current velocities. Unless the pool species are able to exploit another niche dimension, local coexistence for these species is impossible. The slab-rock pools prevalent in the drainages studied by Page and Schemske do not appear to provide a

variety of substrates upon which segregation could occur; these benthic fishes are also unable to divide the water column vertically. The pool species thus appear to be unable to locally coexist and are forced to segregate geographically. Apparently, in each river system the physical conditions vary in such a manner that each pool species has a drainage in which it has the maximum potential. Thus the species form a nonoverlapping mosaic of geographical distribution.

Species Interactions and the Evolution of Cottus in Western North America

From the above treatment, it is apparent that species interactions can drastically affect both the local and regional use of habitat by Cottus and, as in the case of C. beldingi, may act to produce major specializations to allow coexistence. These specializations can in many cases affect species morphology. The possibility therefore exists that species interactions may have significantly affected the evolutionary patterns in Cottus.

The systematic relationships between the Cottus species of western North America have long been of interest and have been the subject of several thorough treatments (Bailey and Dimick 1949; Robins and Miller 1957; McAllister and Lindsey 1961; Bailey and Bond 1963). These treatments, which are based primarily upon morphological data and geographical distributions, have provided workable taxonomic keys for most species (e.g., Bond 1973; Maughan 1978). There is, however, tremendous intraspecific variability in some species. In some cases,

populations that key to the same species appear overall to be more morphologically different from each other than are populations that key to different species. The evolutionary relationships suggested by these keys are therefore questionable.

A perusal of the keys and specimens of Cottus indicates two salient features of sculpin taxonomy: (1) that the characters used to distinguish most species in the keys are regressive (i.e., are noted as "the loss of" a certain body part, or "having fewer" parts of meristic characters) and are thus easily modified morphological traits, and (2) the degree of overall intraspecific morphological variability varies considerably among species (C. E. Bond, K. M. Howe, pers. comm.; T. R. Finger, unpubl. data). Further, the degree of intraspecific morphological variability appears to be related to the potential ability of the species to utilize habitat. Large, dominant species, like C. rhotheus, appear to have relatively low morphological variability (Schultz 1930), although populations isolated in coastal drainages do differ from those of inland waters (Bailey and Dimick 1949). Contrastingly, the less dominant species that are often displaced from their preferred portions of the environment by the dominant species generally exhibit considerably more morphological variability. For example, C. perplexus is an extremely variable species; it demonstrates high morphological variability both within and between populations (Bond 1963). Similarly, C. beldingi exhibits marked variability, both in morphological characters and in localized use of habitat. Specimens

of this species from the Marys River are considerably less elongate than those from the Cascade tributaries of the Willamette River (pers. obs.), and, although C. beldingi is never found in pools in the Marys River, large populations of this species exist in Lake Tahoe (Miller 1951; Baker and Cordone 1969; Ebert and Summerfelt 1969). These patterns of variability may then be related to species interactions as outlined in Figure 25. When they invade different river systems, the species with high potential may exist alone or displace one or more species with lower potential (Fig. 25a). In all cases, they will obtain their preferred portion of the environment. The populations of these species will therefore be subject to less variation in environmental conditions; the lack of a need to adapt to a wide range of conditions could potentially result in less morphological variability. Contrastingly, when species with low potential invade different river systems, they may in some cases obtain their preferred portion of the environment, but will often be displaced from these areas by other, dominant species (Fig. 25b). The populations of the less dominant species therefore will each be subject to different environmental conditions and could be expected to exhibit greater morphological and behavioral variability.

This concept can then be applied specifically to the patterns exhibited by the three species studied in this thesis. Cottus perplexus, C. rhotheus, and C. beldingi do not appear to be closely related (Bailey and Bond 1963), and probably entered the Willamette drainage at different times (Bond 1963). Cottus perplexus appears to

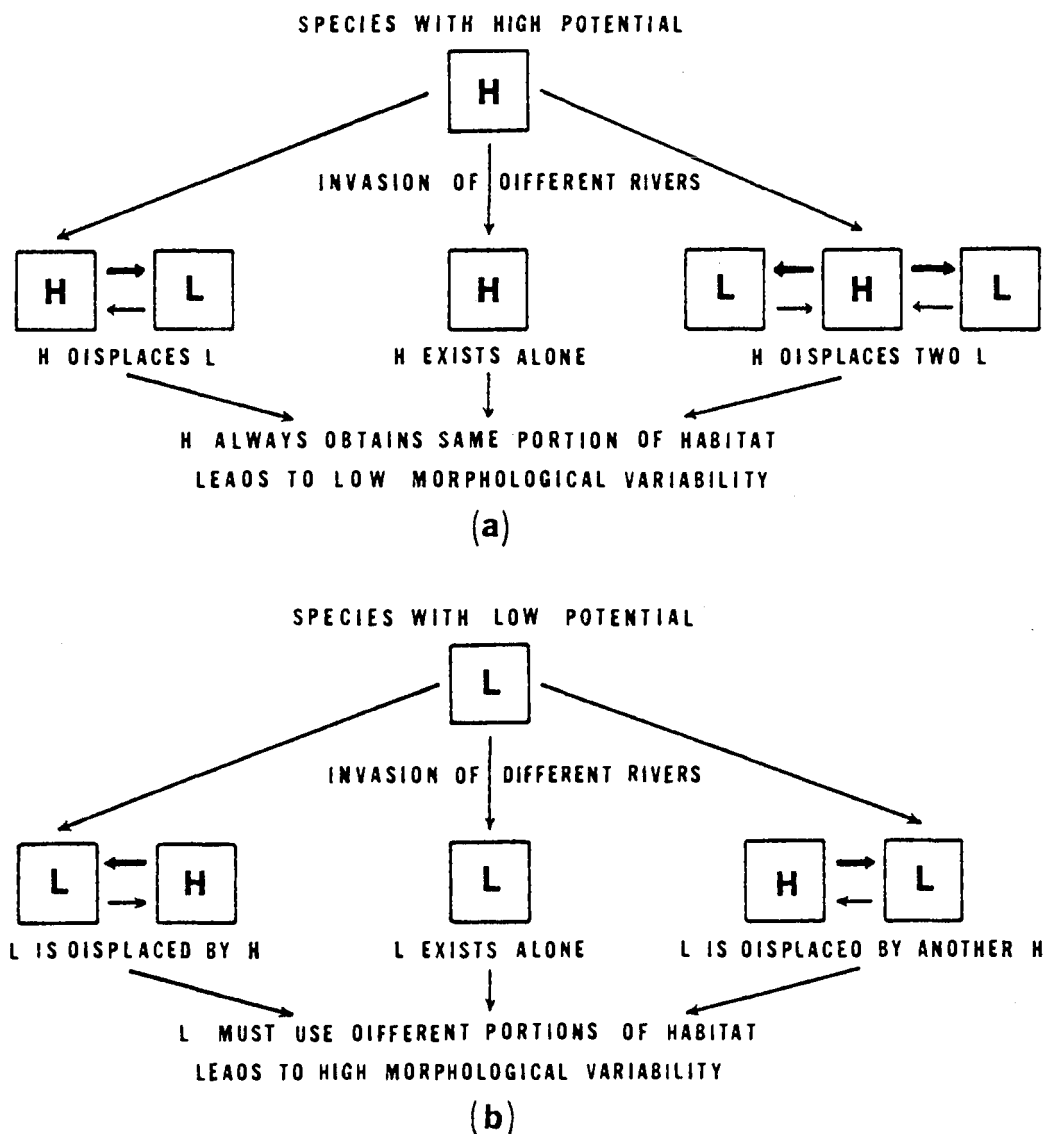


Figure 25. Relations between species interactions and morphological variability in *Cottus*.

- (a) Species with high potential ability to utilize habitat demonstrates low morphological variability.
- (b) Species with low potential ability to utilize habitat demonstrates high morphological variability.

have entered the drainage first, followed by C. rhotheus. Cottus beldingi, generally considered a colder water species, apparently entered last, probably during the cool, glacial period 4000 to 8000 years ago. As the climate changed, the populations of these species were isolated; this isolation was probably most pronounced for C. beldingi. For example, the Marys River is the only Coast Range tributary of the Willamette River that contains C. beldingi. This population is apparently isolated from the others in the drainage by the warmer, lower reaches of the Marys River. Over its wide distribution in the drainage, the low potential C. perplexus coexists with many different combinations of species in a wide variety of dissimilar environments and thus demonstrates tremendous morphological variability. The isolated populations of C. beldingi exhibit a similar pattern. In areas like the Marys River, where it coexists with the dominant C. rhotheus, and where current velocities in riffles in summer are not rapid enough to exclude C. rhotheus, C. beldingi has evolved the rounded, less elongate body form, possibly as a specialization for the burrowing required for coexistence. In other areas, where C. rhotheus does not occur or the current velocities in riffles remain high throughout the year and thus give C. beldingi a refuge, C. beldingi is not forced to burrow and has a more elongated body. Cottus rhotheus is always found in its preferred riffle environment throughout the drainage and thus exhibits low morphological variability.

Although there currently is not an abundance of data to support this hypothesis, the patterns do suggest that a new strategy should be considered to examine evolutionary relationships in the genus Cottus. If the hypothesis is correct, morphological variation in a species of Cottus would not be expected to demonstrate geographical clines, but rather should be more strongly related to the potentials of coexisting species and the ranges of environmental variables, especially current velocity, available in each locale. Systematists interested in Cottus should concentrate on morphological characters most likely to be affected by species interactions, rather than the regressive characters that define the most convenient keys, and examine these characters with regard to variation in the type of coexisting species and the available range of environmental variables among locales.

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APPENDICES

Appendix I. Apportionment of kick net riffle samples and electrofishing pool samples by area and season, and a sample field data sheet.

Riffle Samples

Season	Number of Samples				Total
	Area 1	Area 2	Area 3	Area 4	
Summer	52	64	57	162	335
Winter	22	77	--*	65	164
Spring	50	55	30	116	251
Total	124	196	87	343	750

* Winter sampling in Area 3 impossible due to high water levels.



Pool Samples

Season	Number of m ² Sampled				Total
	Area 1	Area 2	Area 3	Area 4	
Summer	13.4	43.4	43.5	98.0	198.3
Winter	--*	--*	--*	--*	--*
Spring	14.5	26.5	24.0	43.0	108.0
Total	27.9	69.9	67.5	141.0	306.3

* Winter pool sampling impossible in all areas due to high water levels and turbidity.

Appendix I. Continued.

Sample Field Data Sheet

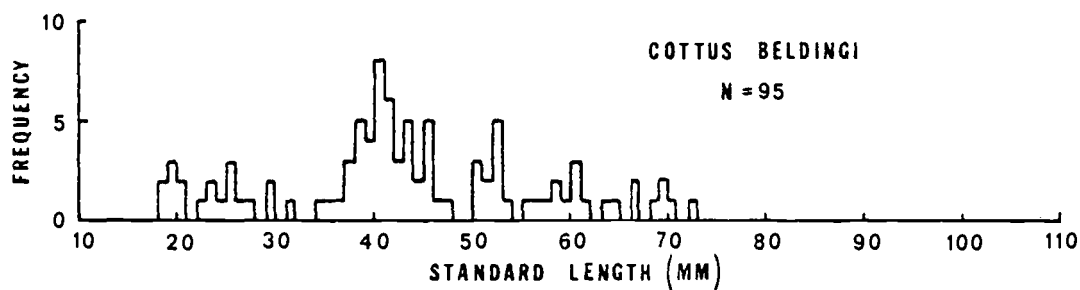
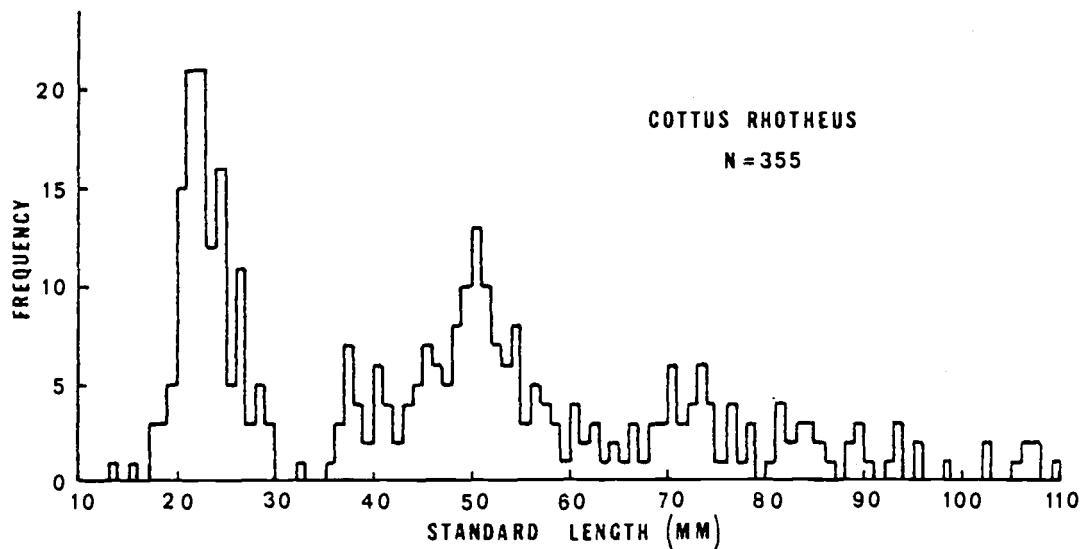
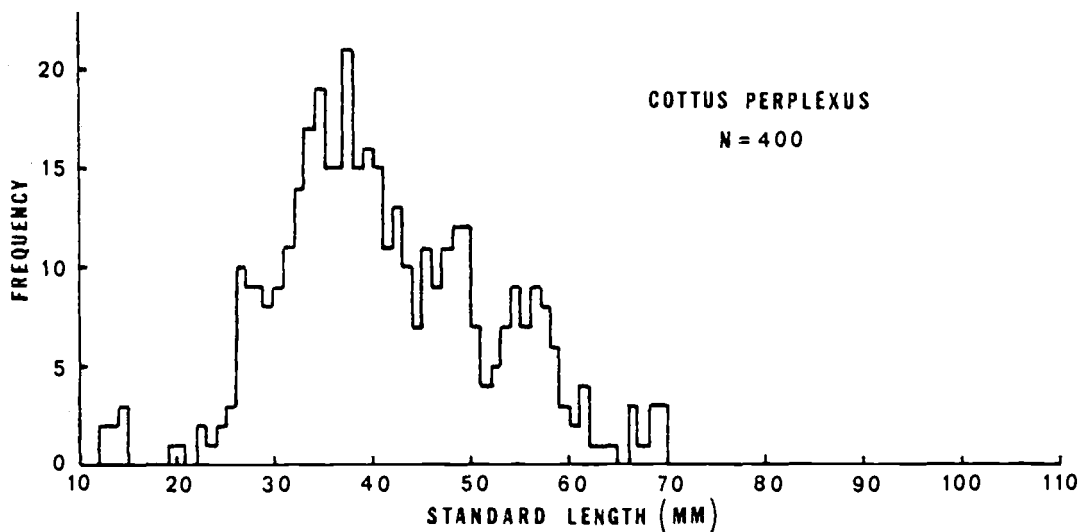
Time <u>1300-1500</u> Date <u>12-X-77</u>	
Sampling Method <u>Kick Net, Shocker</u> Weather <u>Cloudy, Air Temp. 10°C</u>	
Location <u>Marys River 300m upstream from covered bridge (4 km above Wren)</u>	
Sample:	1 2 3 4 5
Site Type	Riffle Riffle Riffle Pool Pool
Temp. (°C)	12°C 12°C 12°C 12°C 12°C
Stream Width	10 m 11 m 8 m 10 m 11 m
Dist. to Shore	3.2 m 0.5 m 1.2 m 0-3 m 2-4 m
Substrate Type	10% 1"-2" 20% 2"-4" 70% 4"-6" 10% wood debris 30% 0.5"-1" 20% 1"-2" 50% 2"-3" 70% 2"-4" 30% 4"-8" 80% 0" (sand) 20% 4"-6" 50% wood debris 60% 0" (silt) 40% 2"-3" 30% vegetation
Current Vel. (clicks/30 sec)	L 32 47 55 M 27 38 61 R 38 52 53 } <0.1 m/sec } <0.1 m/sec
Depth	L 10.2 cm 25.3 cm 5.6 cm 0 cm - 15.3 cm - 32.1 cm - 31.0 cm 15.2 cm - 13.3 cm - 29.1 cm M 15.4 cm 31.2 cm 8.2 cm 0 cm - 14.2 cm - 28.2 cm - 33.0 cm 13.3 cm - 12.1 cm - 15.3 cm R 12.3 cm 33.4 cm 6.3 cm 0 cm - 16.3 cm - 30.3 cm - 29.2 cm 10.2 cm - 13.3 cm - 14.2 cm
Fish Species and Std. Lengths	<u>C. rhotheus</u> 31, 42 <u>C. beldingi</u> 43 no fish <u>C. beldingi</u> 55, 62, 38 <u>C. perplexus</u> 45, 28, 37, 54, 27 <u>C. rhotheus</u> 106 <u>R. balteatus</u> 32, 43, 28 <u>C. perplexus</u> 23, 37, 43 <u>R. balteatus</u> 36, 27, 53, 46 <u>P. transmontana</u> 54
	area:  Total = 6 m ² area:  Total = 5.5 m ²

Appendix II. Maximum temperature longitudinal profile, Marys River system above Philomath, Oregon. Temperatures were taken in midafternoon (1400 - 1800) on 11-VIII-77, after several sunny days of record high temperatures when stream flow was very low. The data therefore probably represent water temperatures that are several year maxima. Air temperature = 37° C. For locations, see Figure 2.

Sites (arranged longitudinally)	Area	Water Temp. (°C)
West Fork, Marys River near headwaters	1	20.5
East Fork, Marys River near headwaters	1	24.0
Marys River at Summit	1	20.0
Marys River at Blodgett	3	20.0
Shotpouch Creek at Burnt Woods	2	23.5
Tum Tum River near Blodgett	3	20.5
Marys River 2 km below Blodgett	3	23.0
Marys River 4 km above Wren	4	25.0
Marys River at Wren	4	27.0
Woods Creek near headwaters	1	17.0
Woods Creek near mouth	2	23.0
Greasy Creek near headwaters	2	22.0
Greasy Creek near mouth	4	25.0
Rock Creek near mouth	4	22.0
Marys River at Philomath	4	27.0

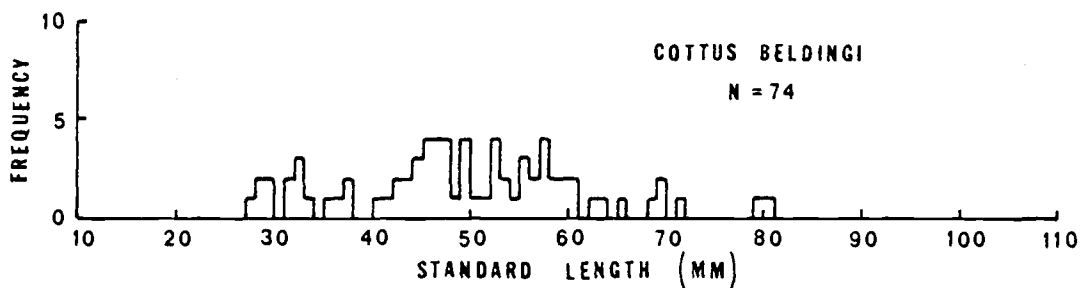
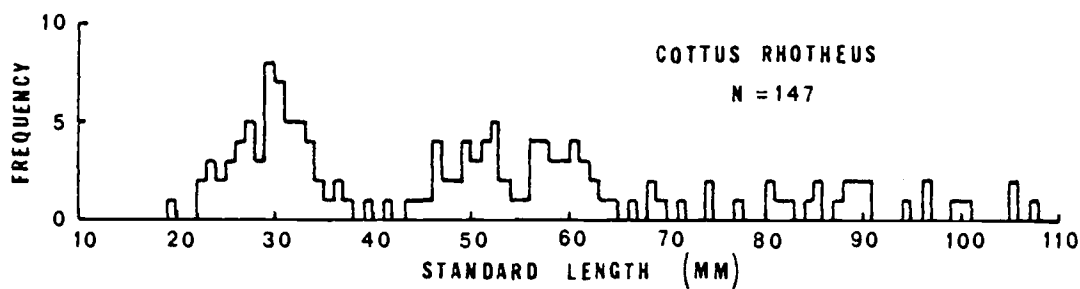
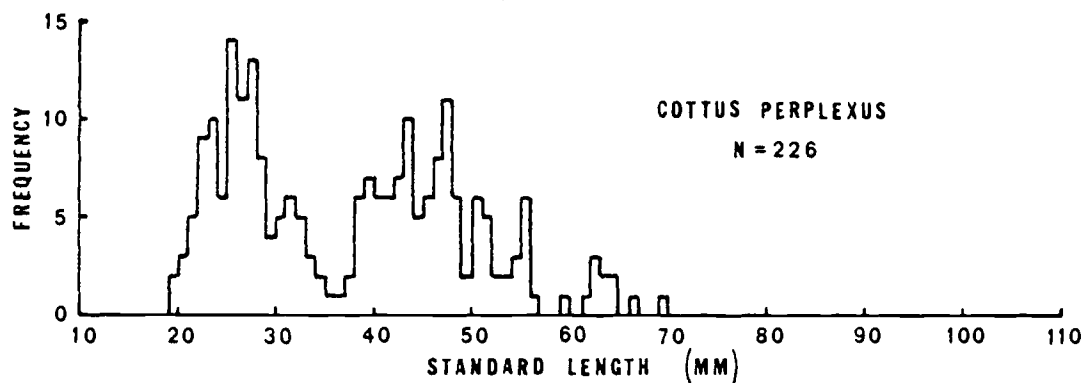
Appendix III. Length-frequency plots of Cottus, Marys River, Oregon. In addition to the fish plotted below, C. rhotheus of 111 mm, 115 mm, and 132 mm standard length were captured in summer.

SUMMER



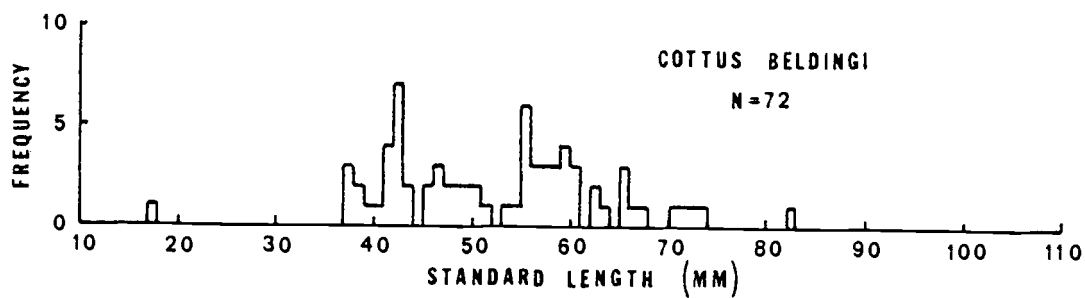
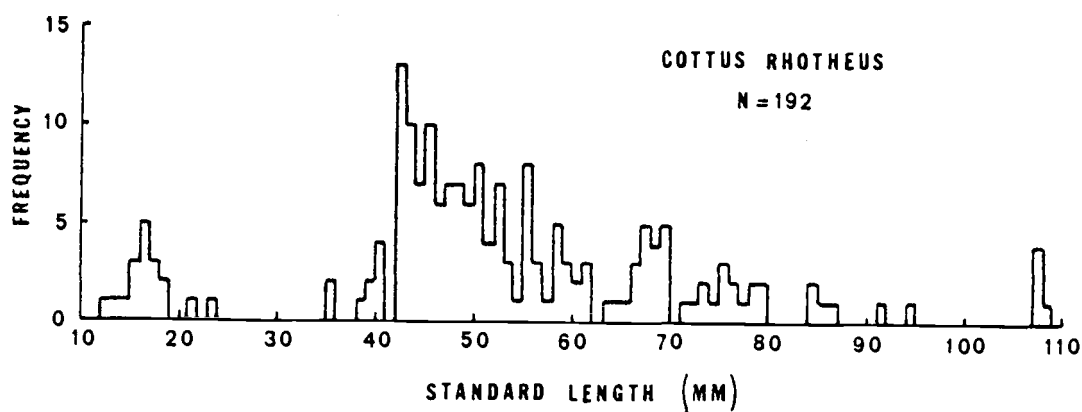
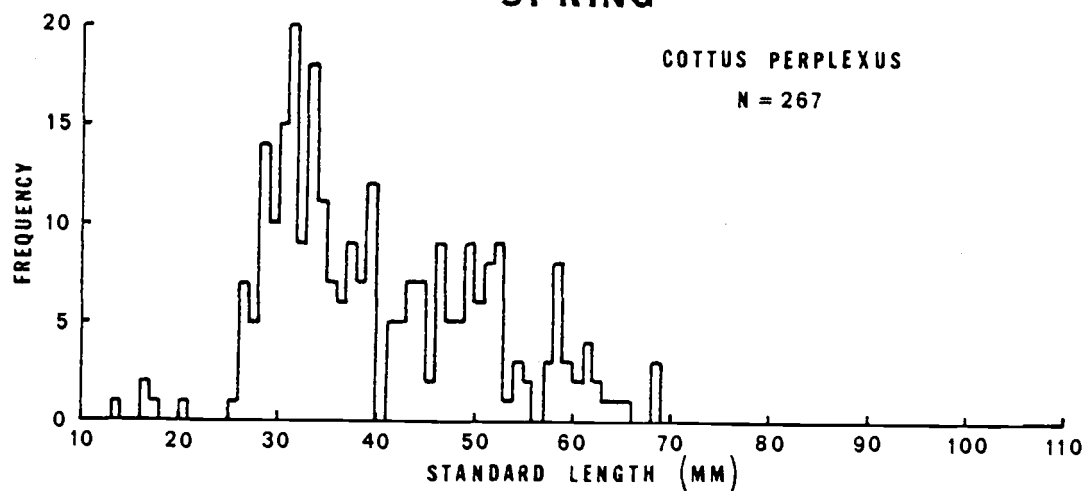
Appendix III. Continued. In addition to the fish plotted below, a *C. rhotheus* of 111 mm standard length was captured in winter.

WINTER



Appendix III. Continued. In addition to the fish plotted below, *C. rhotheus* of 110 mm, 111 mm, 111 mm, 122 mm, and 132 mm standard length were captured in spring.

SPRING



Appendix IV. Weight-length relations used to calculate biomass from standard length. Data used to develop these relations collected from preserved specimens from the Marys River, Oregon. No significant differences were found between weights calculated from these relations and those of live specimens (Appendix V).

Cottus perplexus:

$$W = 1.3044 \times 10^{-5} \cdot L^{3.1538}$$

Cottus rhotheus:

$$W = 9.9060 \times 10^{-6} \cdot L^{3.2115}$$

Cottus beldingi:

$$W = 1.0887 \times 10^{-5} \cdot L^{3.2023}$$

where:

W = weight in grams,

and

L = standard length in millimeters.

Appendix V. Standard length and weight of each fish used in the artificial stream experiments. All individuals were collected from Area 4 sites in the Marys River, Oregon.

Species	Stream	Standard Length (mm)	Wet Weight (gm)
<u>Cottus perplexus</u>	W1	38	1.350
		41	1.410
		44	1.705
		52	3.025
	W2	41	1.474
		39	1.255
		37	1.178
		56	3.610
	E1	43	1.575
		36	0.880
		50	2.620
		54	3.363
	E2	40	1.238
		37	1.015
		38	0.992
		63	5.112
<u>Cottus beldingi</u>	W1	64	5.675
		58	4.010
		55	3.055
		48	2.180
	W2	62	4.700
		58	4.220
		51	2.618
		47	2.210
	E1	63	5.325
		58	4.585
		55	3.545
		50	2.378
	E2	61	4.505
		57	4.218
		52	2.700
		48	2.225

Appendix V. Continued.

Species	Stream	Standard Length (mm)	Wet Weight (gm)
<u>Cottus rhotheus</u>	W1	79	10.240
		85	13.452
		55	3.594
		53	3.103
	W2	76	9.440
		79	9.050
		51	2.380
		55	3.396
	E1	69	6.665
		96	12.735
		55	3.148
		51	2.474
	E2	73	7.673
		85	13.145
		50	2.642
		58	3.538