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MOVEMENTS OF THE GASTROPOD,  
CAMPELOMA DECISUM, IN AN  
ARTIFICIAL STREAM

by

John Badgerow

A Thesis  
Submitted to the  
Faculty of The Graduate College  
in partial fulfillment  
of the  
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John Badgerow

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## INTRODUCTION

### Environmental Factors as an Influence on the Distribution of Stream Benthos

Members of the stream benthos exist under the continuous influence of a host of distinguishable but interrelated environmental factors. These factors may cause movement among the benthos directly, through the application of force, or indirectly, by acting in such a way as to induce the response of movement. In either case, the distribution of the stream benthos at any point in time is the net result of the movements brought about by environmental factors. It is the main objective of the present study to determine the influence of certain of these factors on the movements, and thus the distribution, of a member of the stream benthos - the prosobranch gastropod, Campeloma decisum Say. The rate and direction of movement of the snails was observed under controlled conditions in an artificial stream system. The environmental factors chosen as variables were current velocity, substrate type, and light condition (light versus dark). These three factors were not chosen arbitrarily but rather on the basis of their importance as an influence on movement and on the basis of the extent to which their importance was investigated in other studies on the movements and distribution of Campeloma.

The relative importance of each of several environmental factors as an influence on the distribution of the stream benthos has been the subject of considerable discussion in the literature. It's of obvious value for the present study that this discussion be reviewed, especially as it pertains to Campeloma. The significance of my results, especially in terms of their applicability to observed distributions of Campeloma in the field, is to a large degree dependent upon the relative importance of the factors chosen as variables. In addition, such a review establishes the background necessary for any comprehensive distributional study.

Factors Known or Thought to be Influential in Determining the Distribution of Stream Benthos (Particularly Campeloma) and their Relative Importance

Environmental factors are categorized as abiotic or biotic. Abiotic factors may be considered chemical or physical. It will be stressed now and several times later that these factors are interrelated. They affect each other and frequently interact in their influence upon the distribution of the stream benthos. They are, nevertheless, distinguishable as factors and will be approached independently but with frequent reference to important interrelationships.

### Chemical factors, calcium and other ions

Chemical factors of known or potential importance for the distribution of Campeloma include calcium and other ions, hardness and alkalinity, pH, and oxygen.

Calcium is a chemical factor of particular importance to mollusks as a requirement for shell formation. It is also necessary for animal metabolism and the growth of aquatic plants (Abdel Malek, 1958). Calcium, then, is essential to life in streams but its influence on the distribution of stream benthos is not clear. Calcium concentration and water hardness are closely related and hardness is often measured as parts per million of calcium carbonate. What is known about the distributional importance of calcium applies also to hardness.

Boycott (1936) believes that one of the environmental factors of greatest importance in determining whether or not a habitat is suitable for freshwater mollusks is calcium. Hard water (high calcium content) is undoubtedly more favorable to mollusks than soft water (low calcium content) but it is difficult to assess its importance in nature because comparable habitats tend to differ in many other respects than just calcium content. Also, the influence of calcium content may be disguised or overridden by other factors.

The scale of hardness which humans apply to their water supplies is not very appropriate for use in reference to mollusks (Boycott, 1936). Water for human use is not considered hard unless it contains at least 50 milligrams per liter calcium and soft water usually contains 20 milligrams per liter or less, a concentration which seems sufficiently great for most mollusks and is, to them, hard water.

A biological survey team working in Tennessee found Campeloma decisum in waters ranging from 7 to 135 parts per million calcium carbonate, C. lewisii in waters from 10 to 20, and C. ponderosum in waters from 63 to 70 (Shoup, 1943). This is useful information but it is no proof that these species cannot exist in waters outside the reported concentrations or that calcium content, rather than something else, is the limiting factor. Actually, the calcium content of the water may be of very little consequence to the suitability of a habitat for Campeloma. Morrison (1932) reports that Campeloma is the only member of its family and one of the few freshwater prosobranchs that can tolerate extremely soft water. He believes that Campeloma living under such conditions obtain calcium directly from the substrate rather than from the open water above. This seems particularly feasible for a burrowing snail. Abdel Malek (1958)

mentions the importance of "the calcium content of the substratum, derived from the exchangeable calcium of the colloidal complex, the calcium carbonate in soil lime, and the calcium silicate in rock fragments" in analyzing freshwater habitats. He also finds that "the calcium content of a particular body of water appears to control only the density of the snail population and whether the shells are thick or fragile".

From this discussion it may be concluded that, for Campeloma: 1)there is some minimum amount of available calcium which is essential to life as well as for growth and reproduction; 2)the calcium content of the water is irrelevant if there is a sufficient source in the substrate; 3)it's likely that there are few, if any, streams within the range of Campeloma which are sufficiently low in calcium from one source or the other to be intolerable and, therefore, calcium is probably not an influence in macrodistribution; and 4)of itself, calcium is of little direct influence in determining microdistribution. A relationship has been established between the chemical factor of calcium and the physical factor of substrate type.

Abdel Malek (1958) discusses the importance in the distribution of mollusks of some other ions. Freshwater snails cannot tolerate a very high salt content. Some magnesium is necessary but an excess is harmful. Sodium

may occur as a chloride, sulfate, or carbonate. A high ratio of sodium to calcium is harmful because the sodium ions tend to displace calcium and less of it is absorbed. Small amounts of iron are necessary for algal growth and it seldom occurs in sufficient amounts to be limiting to mollusks. High concentrations of these or other ions may be detrimental or lethal to Campeloma and thus influence their macrodistribution. Such conditions are likely to arise only due to pollution.

#### Chemical factors, hardness and alkalinity

Water hardness is caused by the bicarbonates and sulfates and, to a lesser extent, the chlorides and nitrates of calcium and magnesium (Abdel Malek, 1958). Alkalinity is a more specific term representing the bicarbonate content alone. Both can be expressed as calcium carbonate concentration and, in general, the above discussion on calcium applies to hardness and alkalinity as well. In fact, hardness and the concentration of all ions in water are interrelated. "In naturally occurring hard waters not only are calcium and magnesium present in relatively high concentrations but it is nearly always true that other ions, e.g. chloride, sulphate, and sodium, are also more abundant than they are in soft waters. Hard water has, therefore, not only more calcium than soft water but nearly always more of

several other ions, and also a higher osmotic pressure" (Hynes, 1970).

Hynes (1970) concludes "that water hardness is a controlling factor in the ecology of at least some stream invertebrates". However, there is no evidence to date that Campeloma is among them. Harman and Berg (1971) found C. decisum in central New York waters ranging in alkalinity from 58 to 159 (mean 88) parts per million calcium carbonate. They concluded from their survey that hardness and alkalinity do not limit the distribution of C. decisum or any of the other mollusks they encountered.

#### Chemical factors, pH

Morrison (1932) found Campeloma decisum in Wisconsin waters ranging in pH from 5.68 to 8.37 and C. milesii in waters from pH 5.86 to 8.0. Harman and Berg (1971) collected C. decisum from waters in central New York with a range of pH 7.3 to 8.5 (mean of 7.9). These findings indicate a wide range of tolerance for C. decisum. There is no evidence that pH is a factor limiting the distribution of C. decisum (Harman and Berg, 1971). Indeed, pH is rarely a limiting factor for snails in general (Abdel Malek, 1958) and there is little more than occasional circumstantial evidence of the importance of pH, as such, for stream-dwelling invertebrates (Hynes, 1970). The chemical factors on which pH is dependent, such as

"alkali reserve, carbon dioxide content, sunlight, photosynthesis with the active removal of  $\text{CO}_2$  and the production of  $\text{O}_2$ , and the character of the substratum are more important than pH alone" (Abdel Malek, 1958). An additional problem in the use of pH readings as an indication of the suitability of a habitat lies in the fact that pH often varies from one location to another within the same habitat and with the time of day at a single location (Abdel Malek, 1958; Boycott, 1936).

#### Chemical factors, oxygen

Harman and Berg (1971) found Campeloma decisum in waters ranging from 3.6 to 10.8 parts per million dissolved oxygen (mean of 9.6). They report that "the only chemical factor monitored that seems to limit snail distributions in central New York is low concentrations of oxygen". However, the low oxygen habitats are in marshes and swamps, not streams, and prosobranchs such as Campeloma may be absent from such habitats only because of dispersal problems or a lack of tolerance of the periodic water shortages occurring in swamps and marshes (Harman and Berg, 1971). In streams, low concentrations of oxygen are a rarity and, except in some cases involving pollution, oxygen is seldom a factor in the ecology of stream invertebrates (Hynes, 1970).



Any existing influence of oxygen on the distribution of stream benthos is interrelated with the physical factors of substrate type and current velocity (Eriksen, 1966; Jaag and Ambuhl, 1964). As a matter of fact, oxygen concentration and current velocity are so closely connected in their physiological importance that it is inadequate and even incorrect to consider the two factors separately. And for a burrowing organism such as Campe-loma, substrate type is intimately related to oxygen concentration as well. For these reasons, the importance of oxygen will be discussed further in connection with both current velocity and substrate type.

Chemical factors as a whole appear to have little influence in determining the macrodistribution of stream benthos in the majority of natural situations (Harman and Berg, 1971; Macan, 1961). Water pollution can result in exceptions to this generality. The influence of chemical factors on microdistribution must be minor and subordinate to the influences of some physical and/or biotic factors, as will be further shown. It should be remembered that there are numerous and complex interrelationships among the various chemical factors and among all the factors which make up the environment. The importance of any one factor in limiting distribution may be made greater or lesser by variations in one or more of the others.

Physical factors, depth

Some of the water depths at which Campeloma has been collected are reported in Table 3. They range from two inches or less to eight feet. Gastropods are generally found in shallow water, usually less than two feet deep (Boycott, 1936). Abdel Malek (1958) and Boycott (1936) state that rapid fluctuations in water level hinder the establishment of populations of snails or keep such populations small. Medcof (1940), however, found Campeloma in a mill pond from the margin to depths of ten or twelve inches and they remained within this depth range by horizontal movement as the water level (and thus the shore line) of the mill pond fluctuated rapidly. In streams, particularly, the influence of depth on the distribution of the benthos is clearly related to the factors of current velocity and substrate type (Brown, 1971; Harman, 1972). In riffles, Egglshaw (1969) found very little significant association of benthic invertebrate species with water depth. In the "deep, quiet pools" of streams, Harman (1972) found a "littoral silt and detritus association" of which C. decisum was a typical member. He also found C. decisum in "eulittoral silt and detritus", a substrate type found along the shallow, quiet margins of streams. Thus depth, of itself, appears to have little or no direct influence

on the distribution of stream benthos but is an integral part of other factors, such as current velocity and substrate type, which may exert a major direct influence.

#### Physical factors, temperature

Temperature has an important influence on the distribution of stream benthos (Hynes, 1970; Jaag and Ambuhl, 1964; Minshall, 1969). Life histories are often regulated by temperature and each stage in an organism's life history may have a different susceptibility to extremes in temperature (Hynes, 1970; Macan, 1961). High temperatures are more limiting than low for snails (Boycott, 1936) but in temperate climates the rate and extent of variation is as important as the maximum (Hynes, 1970). Oxygen concentrations and respiration rates are related to water temperature and some species in streams may be limited in this fashion by temperature (Hynes, 1970). But temperature is much more limiting to snails living in shallow water at the edge of ponds, lakes, and rivers than in the running water of smaller streams (Boycott, 1936). The influence of temperature on the distribution of stream benthos is primarily on the macrodistribution level or higher (Jaag and Ambuhl, 1964). Thus, the geographical range of Campeloma may well be limited, at least in part, by temperature. The distribution of Campeloma along the length of a single

stream may be under the influence of temperature in some instances. It appears, however, that temperature is rarely a factor having any great influence on microdistribution.

Physical factors, light intensity

"A few investigations have indicated that there is a definite correlation between shade and the occurrence or abundance of certain species along the lengths of variously shaded streams" (Hynes, 1970). This has not been investigated in the case of Campeloma. The main importance of light to snails, as well as the other invertebrates, is through its influence on aquatic plants (Abdel Malek, 1958; Boycott, 1936; Brown, 1971; Hynes, 1970). Sunlight encourages the growth of aquatic macrophytes and algae and the high oxygen concentrations from photosynthesis increase the decomposition rate of detritus. Shade discourages most aquatic plant growth and leaves and other parts of the shade-providing plants along the banks may fall into the water and become a food source for the stream benthos. Thus light intensity is interrelated with oxygen and food and with temperature as well. For Campeloma, living aquatic plants are not a source of food and, as discussed earlier, oxygen is seldom limiting in the flowing water of streams. Allochthonous detritus is undoubtedly a major food source for Campeloma but

there is no evidence that the snails are limited to shaded streams or stream sections by this factor. Light intensity is unlikely to have much direct influence on the distribution of Campeloma in streams although it may be found to have some influence indirectly, that is, in correlation with food, oxygen, and temperature.

#### Physical factors, current velocity

Current velocity is widely considered to be a factor of major importance in influencing the distribution of stream benthos (Cummins, 1962, 1964; Hynes, 1970; Jaag and Ambuhl, 1964; Kamler and Riedel, 1960; Lillehammer, 1966; Linduska, 1942). Predominating species and even entire communities may change with changes in current velocity (Hynes, 1970). Lillehammer (1966) compared two sites in a stream which were similar in all respects except current velocity and found a great difference in the faunal composition.

Whether current velocity exerts a greater influence on macrodistribution or on microdistribution is not clear. It may be a factor of considerable, if not primary, importance in both cases. Cummins (1964) includes current velocity among the factors "of primary importance in determining the microdistributions of benthic invertebrates". Cummins and Lauff (1969), however, conclude that although current velocity "may

limit the general ranges of habitat tolerance (macrodistribution), it seems that substrate particle size or food supply probably exert primary microdistributional influences". Jaag and Ambuhl (1964) designate current as the most important factor influencing microdistribution.

Some species of stream invertebrates have been found to prefer a certain range of current velocity (Hynes, 1970). The tolerated range seems to be much wider than the preferred range. Macan (1963), in reviewing several field and laboratory studies, states that although "each species was most abundant at a certain current-speed, nearly every one was found over a very wide range of velocities". Distribution can definitely be limited by high current velocities (Abdel Malek, 1958; Allen, 1959; Boycott, 1936; Hynes, 1970; Macan, 1961). Allen (1959) found a correlation of stream fauna with maximum current velocity (although below the significant level) and no correlation with the total area of stones or the size of the largest stones on the stream bed. A very high current velocity will eliminate nearly all species and areas of low current may be lacking many species if those areas are subject to periodic spates (Hynes, 1970). This limit to distribution certainly applies to mollusks (Boycott, 1936). Thus, the distribution of stream benthos may be current-limited by selection of a preferred range or by the restrictions imposed

by high velocities, either continuously or during spates. Macan (1963) concludes that distribution must be influenced by both these alternatives.

The influence of current velocity on the distribution of stream benthos is interrelated with the influences of several other factors. According to Brown (1971), "the effect of current on the distribution of organisms must be assessed along with other factors". One of the closest and undoubtedly the most important of these interrelationships, in terms of distribution, is that between current velocity and substrate type (Brown, 1971; Butcher, 1927, 1933; Cummins, 1966; Harman, 1972; Harman and Berg, 1971; Kamler and Riedel, 1960; Macan, 1961; Percival and Whitehead, 1929; Scott, 1966). "Current is of primary importance in determining the main types of substratum" (Macan, 1961). Current may influence distribution directly, as discussed above, or indirectly through its effects on the substrate. The nature of the substrate, in turn, greatly effects the current conditions at its surface. For these reasons, current and substrate are usually considered together (Cummins, 1964) and, except as a matter of convenience for discussion, cannot be considered separately in their influence on distribution (Linduska, 1942; Macan, 1963).

As current velocity increases, substrate particle size increases (Eriksen, 1966). Thus Campeloma, which is

usually found burrowed in a fine substrate which it is capable of penetrating, is also usually found in microhabitats where low current velocities are prevalent. In addition, in areas where the general stream flow is at high velocities and the substrate coarse, numerous microhabitats exist at and in the bottom which provide conditions of low current velocity. This has been well described by Jaag and Ambuhl (1964), as follows:

In every turbulently flowing system, marginal effects develop in what are called boundary layers, named after their discoverer as Prandtl's layers. Close to the substratum, movement of the water gradually ceases owing to friction and a boundary layer is constituted in which the flow is strongly retarded, until ultimately, it is stagnant. Moreover, zones of dead water are formed in cracks, fissures and spaces between the individual stones of the stream bed and the like, as well as behind every protrusion into the stream, so that to a great extent the dead water is separated from the freely moving water. As can be observed in the streams themselves as well as by experiment, it is in such dead waters and in sediments that the greater part of rheophilic life is spent. Hydraulically speaking the inside of plant clusters, moss and algae as well as fragments of roots, rotting leaves, etc., are to be classed with the dead water.

It is clear from this description that the bottom of a stream consists of a mosaic of velocity conditions in which nearly still or still water can be found, even in rapidly flowing stream sections. The distribution of the stream benthos, with their various behavioral and physiological adaptations, is closely related to this mosaic of current conditions (Eriksen, 1966; Jaag and Ambuhl, 1964).



Although only the very young of Campeloma would be small enough to utilize boundary layers, they are certainly capable of using many dead water zones for movement and shelter in areas where the current would otherwise sweep them away. It is in these ways that current and substrate are closely interrelated factors and of primary importance in influencing the distribution of the stream benthos, including Campeloma.

Food supply is another factor contributing to the influence on distribution of both current velocity and substrate type. The deposition in the substrate of detritus, the food source of Campeloma, is largely dependent upon current velocity (Buscemi, 1966; Butcher, 1933; Kamler and Riedel, 1960). Thus whatever influence food supply has on the distribution of Campeloma is interrelated with the influence of current velocity. Current velocity itself, the thickness of boundary layers, and the surface configuration of the substrate all influence the rate of deposition of detritus (Buscemi, 1966). Organic detritus is of low density and is deposited in the greatest amounts in the fine substrates, such as sand, mud, or silt, which are found in areas of low current velocity, particularly the nearly still water of pools (Butcher, 1933; Kamler and Riedel, 1960).

Yet another factor, oxygen, should be included in the complex of interrelationships among current,

substrate, and food supply. Oxygen may not be a factor of primary importance in influencing distribution, as has already been discussed, but it is a factor of sufficient import to merit further mention here. Higher current velocities result in coarser substrate types and more turbulent flow over the bottom (Eriksen, 1966). This causes mixing of the water, providing a well oxygenated supply to the benthos. Lower current velocities result in finer substrate types, with less turbulence and mixing, and a greater accumulation of organic detritus. Thus there is not only a poorer oxygen supply but also a higher oxygen demand in areas of lower current velocities. Superimposed upon this picture, and of particular importance for a burrowing form such as Campeloma, is the influence of substrate particle size and current velocity on oxygen concentrations within the substrate. In general, oxygen concentration decreases with decreasing particle size in stream substrates (Eriksen, 1966). This is due to the low permeability of fine substrates and mixed substrates containing fine particles. Stuart (1953) found that current through permeable gravel is dependent more upon the stream gradient than upon the current velocity of the stream. Thus the movement of water and dissolved oxygen into and through the substrate is controlled more by the nature of the substrate than the velocity of the current. Whatever influence oxygen

has on the microdistribution of Campeloma is closely related to the current velocity in the case of exposed individuals and to the substrate type in the case of those snails which are able to be and are buried in the bottom. And the composition of the substrate itself is to a great extent determined by the current.

Current velocity influences distribution directly and through its relationships with other factors. Current velocity itself is determined by a number of factors which vary in their relative importance from place to place in a stream. These factors include substrate type, aquatic vegetation, turbulence, turbidity, gradient, discharge, and water temperature (Minckley, 1963). Many of these factors, in turn, are interrelated. I have attempted to establish the great importance of current velocity, as a physical factor, in influencing the distribution of stream benthos, particularly Campeloma. Discussing environmental factors separately is an artificial but highly convenient approach. I have attempted to coordinate my discussion of the influence of current velocity with other factors with which it is inseparably linked in natural stream ecosystems.

#### Physical factors, substrate type

Substrate type is a factor of great and sometimes primary importance as an influence on the distribution of

stream benthos (Cummins, 1962, 1964, 1966; Hynes, 1970; Macan, 1961). It is a factor of such prevalent importance that it "can serve as a common denominator in the benthic ecology of lotic waters" (Cummins, 1966). Nearly all thorough field studies in lotic ecology reveal that some invertebrates are only found on or in a particular substrate type and others are at least more numerous on a particular substrate type (Hynes, 1970). Frequently found correlations between the distribution of benthos and substrate type indicate that many species possess behavior patterns which enable them to select optimal substrates (Macan, 1963). One of the earliest and most thorough of such studies was that of Percival and Whitehead (1929), who correlated the distribution of nearly every benthic species in a stream with the types of substrate.

I have already discussed the great extent to which the composition of the substrate at any locale in a stream bottom is determined by the current velocity over that locale. Gradient, turbulence, and discharge are factors which should be considered as integral parts of current velocity itself and, as such, act upon the underlying strata over which a stream flows to determine the make-up and distribution of substrates (Minckley, 1963). Aquatic vegetation and other obstacles to current,

whether natural or unnatural, act to modify the influence of current on the substrate. The two basic types of stream macrohabitats are riffles, which are characterized by high current velocities and gravel or cobble substrates, and pools, which are characterized by low current velocities and sand or silt substrates (Cummins, 1964). Within riffles and pools there are, on a finer scale, more macrohabitats containing, in turn, numerous microhabitats. The areas downstream from outward bends of the stream bank (widening of the stream) or large rocks and other such obstructions are sheltered, for some distance, from the direct effects of the current (Kamler and Riedel, 1960). In these areas, the finest substrates (silt and detritus) will be deposited in the dead water zones near the bank or immediately downstream from the obstruction. The substrates will tend to become progressively coarser proceeding out from the bank or downstream from the obstruction, due to the progressively greater current velocities. These areas of relative shelter from the current, macrohabitats, include areas having sand-silt-detritus substrate types, which are microhabitats typically selected by Campeloma. Such microhabitats are also commonly found in stream pools. Although current velocity may exert a direct influence upon the distribution of stream benthos, its indirect effect, the determination of substrate type, appears to

be more important in the distribution of many, if not most of the benthic species, including Campeloma. "Since the nature of the bottom can so profoundly affect the rate of flow of water it appears that stream flow, as such, would necessarily be of secondary importance to bottom-dwelling forms" (Linduska, 1942). This is particularly the case for an animal such as Campeloma, which spends much of its time buried in the substrate, well removed from the stream current.

On the largest scale, entire streams or major sections of a stream, the macrodistribution of the benthos is probably determined by a chemical or physical factor other than substrate (Cummins and Lauff, 1969). But macrodistribution on a smaller scale, as between riffles and pools within a stream section, is often strongly influenced by substrate type. The microdistribution of stream benthos is probably influenced primarily by substrate type or food supply. There is such heterogeneity of conditions, even in an apparently uniform bottom area, that this is possible. "Close examination of any patch of stream-bed at once shows that even within a small area there are very great differences from point to point in the type of environment" (Allen, 1959).

The influence of food supply on the distribution of stream benthos is a topic to be discussed in a following

section. Since this biotic factor is closely related to the physical factor of substrate, however, I will discuss some aspects of this relationship here. "The substratum is the place where most animals find their food" (Macan, 1963). In streams, food chains are based on the type of substrate (Cummins, 1966). Thus, the stream fauna obtains its food either directly from the substrate or by preying upon animals which do so. The distribution of food materials in the substrate represents an indirect influence of substrate upon the distribution of stream benthos (Cummins, 1962). The finer substrates, mud, silt, and often sand, are the parts of the stream bed richest in detritus and provide the microhabitats most favorable to detritivores such as Campeloma (Brown, 1971). The precipitation and absorption of colloidal organic matter is greatest among these substrates (Butcher, 1933). Settling erosion silt carries organic matter to the stream bottom with it and such deposits are "much richer in bacteria than either the river water above these deposits, or the adjacent bottom areas of sand or gravel" (Ellis, 1936). These fine substrates appear to be favored by Campeloma and, although the influences of substrate, current, and food on distribution may be discussed independently, Campeloma are found in such areas primarily because of the combined and interrelated influences of all three.

Some aspects of the relationship of substrate type with oxygen concentration in influencing distribution have been discussed under the heading of current velocity. Both the availability of oxygen and the rate of oxygen consumption by burrowing animals may vary with substrate particle size (Eriksen, 1966). Buried Campeloma, like burrowing mayflies, are limited to an interstitial respiratory environment. Compacted fine sediments not only contain a poor supply of dissolved oxygen but they also require an increased rate of oxygen consumption on the part of animals attempting to penetrate them. Campeloma may tend to avoid such substrates altogether or traverse the surface without burrowing.

Boycott (1936) found that substrate type is an important factor in the distribution of freshwater mollusks. Harman and Berg (1971), in their thorough and extensive study of the mollusks of the central New York region, concluded that "each species of freshwater snail . . . seems to occur with a fair degree of consistency on a particular substrate or combination of substrates. Other conditions may tend to limit a species secondarily, but apparently the presence of a particular substrate gives a certain species the potential for colonizing a given habitat". Campeloma decisum was among these species. Lillehammer (1966) and Scott (1966) were both able to correlate the distribution of mollusks with



substrate types. In fact, freshwater mollusks exhibit habitat selection primarily on the basis of substrate type (Baker, F. C., 1918). Harman (1972) summarized the effects of substrates on freshwater mollusks, including Campeloma decisum, based on collections and observations made in central New York State since 1966. The mollusks exhibited distinguishable preferences for particular substrate types. For snails, the overall species composition and the most common species of a biotope (a term similar in meaning to microhabitat) reflect the nature of the substrate. The various substrates found in streams are stratified horizontally and vertically by the current. The distribution of mollusks corresponds to these stratifications. "This hypothetically simple picture is complicated by all obstructions that alter current velocity, and therefore substrate pattern, causing a mosaic of mollusk demes throughout the typical stream". He concluded that "under normal conditions the occurrence and local distribution of Mollusca within freshwater habitats are primarily determined by the substrate types and patterns in those environments".

If mollusks in general are limited in their distribution primarily by substrate, it seems that this factor should be of even greater consequence in the distribution of burrowers such as Campeloma. Indeed, members of the infauna are more restricted in their range of suitable

substrates than members of the epifauna (Holme, 1954). The surface and the subsurface of a substrate are two distinct habitats (Minckley, 1963). Quite apart from the conditions at the surface, the penetrability of a substrate and substances found within it can both influence the distribution of burrowing benthos (Holme, 1954). For an animal such as Campeloma the substrate can be more than a surface to cling to or move over; once penetrated, the substrate becomes the very medium in which the snail exists and in which it finds not only shelter but oxygen, food, and the other necessities of life as well.

#### Biotic factors, parasitism

Parasites exert a direct and often important effect on many members of the lotic benthos, including Campeloma. Both ectoparasites and endoparasites may have an effect on snails that is harmful both mechanically and physiologically (Abdel Malek, 1958). The known and possible parasites of Campeloma may limit the abundance of Campeloma in some instances but it seems likely that the complete extermination of a natural population by parasites is a rare occurrence. There is no evidence to date to justify the conclusion that the distribution of Campeloma is limited by parasitism as a biotic factor, although it may occasionally have some influence on distribution.

### Biotic factors, predation

In a few instances, a major influence of predation upon the distribution of some members of the stream benthos has been clearly established (Hynes, 1970). It is a factor operating in lotic communities but its influence on distribution in general has not been very extensively investigated and therefore its importance remains uncertain. Laboratory studies have established the voracity of several predators of snails (Abdel Malek, 1958), but their importance under field conditions of much greater complexity is not so well understood. Predators of Campeloma are known but the degree of importance of their influence on the distribution of natural populations has not been established, nor scarcely investigated. A review of the literature and my personal field experience indicate that predation is a factor of negligible importance in the distribution of Campeloma but this is a matter that needs much further investigation.

### Biotic factors, competition

Competition is another biotic factor which may influence the distribution of stream benthos. In the literature on lotic ecology there are "some fairly well-established examples of competitive exclusion by

closely related species" (Hynes, 1970). Chemical or physical factors may have an indirect influence on distribution by selectively favoring one or more species in competition with others. Macan (1961) mentions this as a possibility in the case of temperature. Boycott (1936), in his review of the habitats of freshwater mollusks in Britain, concludes that "there are indications that the habitats of a few species are partly determined by competition with other Mollusca, but in general this is unimportant". Harman (1972), however, found instances of competitive exclusion among the mollusks in two of three large lakes in central New York State; Skaneateles Lake, Otsego Lake, and Oneida Lake. It was especially apparent in Skaneateles Lake, somewhat so in Otsego Lake, and mostly absent from Oneida Lake. In Skaneateles, the mollusks are distributed along horizontal strata of substrates around the lake. The species living on each substrate type have access to nearly all of that substrate type, all the way around the lake. Thus species with similar habitat preferences, and no physical factors hindering contact with each other, may come into severe competition. The substrate patterns in Otsego are similar to those in Skaneateles except that they are fragmented with greater frequency by aquatic macrophytes. Competition is reduced and species diversity is greater. "It is postulated that lakes like Oneida,

which have complex patterns of substrate and relatively irregular shore development, enable many demes of ecologically similar species to thrive without actually coming into contact with each other. Competitive exclusion is therefore reduced and species diversity is greatly increased". Streams, especially smaller streams, tend to have more complex substrate patterns than lakes, even lakes like Oneida. In streams, therefore, competition can be expected to be a factor of only minor importance in influencing the distribution of mollusks. Campeloma, which is the only burrowing gastropod found in its range, would seem to be largely free of competition from other gastropods for that reason. I have found C. decisum coexisting in close association with fingernail clams. In addition, there is nothing in the feeding habits or other aspects of the biology of Campeloma to suggest that it would be likely to encounter much competition.

#### Biotic factors, food supply

Food supply is considered a factor of primary importance in influencing the distribution of freshwater benthos (Cummins, 1962; Hynes, 1970; Macan, 1963). Indeed, the availability of food is a factor of obvious importance to all animals. As far as freshwater animals are concerned, "there are probably species in all groups

whose distribution is related to their food supply" (Macan, 1963). Although food is a necessity of life, it limits the distribution of a given species only to the extent that the correct kind is available in sufficient amounts. "Generally speaking species occur, or are common, only where their food is readily available, but it should not be forgotten that few running-water invertebrates are very specialized in their diets" (Hynes, 1970). Food supply is a factor of primary importance as an influence on microdistribution as well as distribution in general, along with the interrelated factors of current velocity and, especially, substrate particle size (Cummins, 1964; Cummins and Lauff, 1969). The distribution of primary consumers (which includes Campeloma) in a stream can be correlated with the distribution of allochthonous and autochthonous detritus (Minckley, 1963). Such generalizations are common in the literature and there are many studies to support them. For example, Egglisshaw (1969) and Percival and Whitehead (1929), in extensive studies on streams with stony beds, found considerable correlation of the distribution of the benthos with detritus. But, concerning specifics, "little is actually known about the role that sedimentary organics may play in the distribution and abundance of the stream fauna" (Buscemi, 1966). This matter has never been investigated to any depth for Campeloma.

The relationship of current velocity with the rate of deposition of detritus in the stream bed has already been discussed under the headings of current velocity and substrate type. Even where current velocity has a direct, primary influence on the distribution of the benthos, food supply can act as a factor modifying this influence (Brown, 1971; Macan, 1963).

The relationship of substrate type and the distribution of food, as detritus, has also been discussed in preceding sections. The distribution of bacteria, also an important food source in freshwater ecosystems, is related to substrate type as well. Marzolf (1966) was able to correlate the distribution of a burrowing amphipod with the number of bacteria in the substrate but not with substrate particle size or organic content as such. He found that numbers of bacteria tend to increase with decreasing substrate particle size, probably due to the increased surface area and amounts of organic material in finer substrate types. Erosion silt deposits tend to have larger populations of bacteria than either the water of the stream or other substrates (Ellis, 1936). Campeloma has been described as coprophagous and as a detritivore, using food sources which are typically rich in bacteria. The snails may obtain as much or more nutrition from the associated bacteria as they do from the organic matter itself. Campeloma collected for the

present study were found in the immediate vicinity of, rather than directly on, the dog dung bait. The closely related Viviparus is known to have a suspension feeding mechanism. (Owen, 1964). These facts lend support to the idea that bacteria may constitute an important part of the food source of Campeloma. If this is so, the distribution of bacteria, a factor related to substrate type, may play a major role in the influence of food supply on the distribution of Campeloma.

Substrate type and food supply are closely related in their importance to the benthos. A major proportion of certain substrate types may consist of organic rather than inorganic material and nearly all substrates include some amount of organic material. It is thus a characteristic of substrates and the kind or amount of organic material present may be the basis for a description or definition of substrate type. This is just what Harman (1972) did for his study of the effects of substrates on freshwater mollusks. He established five substrate types. Two of these, "eulittoral silt and detritus" and "littoral silt and detritus", consist of "fine organic and inorganic materials" and another two are defined as "autochthonous organic matter - aquatic plants and their decaying remains" and "allochthonous organic matter - decaying terrestrial plants and leaf litter". The fifth substrate type is "clean cobble". Thus two of the five



substrate types are based partially and another two entirely on organic matter. It follows that Harman's conclusion that substrate type plays a role of primary importance in influencing the distribution of freshwater mollusks, discussed in the present paper in the section on substrate type, involves the incorporation of the role of food supply. These two factors are indeed important and very closely related. Once again, treating them separately is more a matter of convenience for discussion than the reflection of a natural dichotomy.

The influence of substrate particle size on distribution may be indirect, acting through the relationship between substrate particle size and the distribution of food materials within the substrate (Cummins, 1962). Also, the factor of food supply may alter patterns of distribution influenced primarily by current velocity and substrate type (Macan, 1963). If the food of an organism can be found over a range of current-substrate conditions, then substrate particle size may have an influence secondary to that of food supply, at least in terms of microdistribution (Cummins and Lauff, 1969). In other words, in some situations food supply may influence distribution within a broader set of limits provided by substrate type or the current velocity-substrate type complex. And the converse of this may also occur. These are possibilities delineating the relative importance and

mode of action of food supply as an influence on the distribution of benthic species.

The quantity of food available to the benthos may be a limiting factor at both ends of the spectrum - too little and too much. For bilharziasis vector snails, which feed on periphyton, "both the density of the snail population and the size of the individuals are directly correlated with the amount of food available" (Abdel Malek, 1958). Some organic pollution can be beneficial to snails but there is a limit above which it becomes detrimental (Muirhead-Thomson, 1958). Buscemi (1966) finds that "it is suggested that a critical upper level exists for the concentration of total organic matter which will act as a limiting factor on populations of benthic filter feeders and browsers". Benthic animals will seldom be found for long in places where their food is absent or at inadequate levels. At high concentrations of organic matter, there may exist an inverse relationship between the distribution of the benthos and organic matter. At levels in between, the relationship may tend to be direct.

For Campeloma, food supply appears to be at least an equal partner with each of the closely related factors of current velocity and substrate type as an influence on distribution. The quiet water and fine substrates in which Campeloma is typically found represent habitats

which are also typically rich in Campeloma's food - detritus and associated bacteria. Aggregations of Campeloma in streams have been found on and near rotting logs, dead animals, and fecal matter. Thus food supply is an important factor in both macrodistribution and microdistribution. Whether or not it is usually more important than substrate type or current velocity is perhaps a moot point, since the influences of all three are so thoroughly interwoven. They form a complex which is itself unquestionably of primary importance as an influence on the distribution (especially microdistribution) of Campeloma and within which the relative importance of each factor varies with place and time.

#### Environmental Conditions Characteristic of Observed Habitats of Campeloma

The preceding discussion on environmental factors of influence in determining the distribution of Campeloma leads to the question of what sort of environmental conditions typify the habitats in which the snails have been found. There is an extensive literature on this topic (which will be reviewed in detail in a later section of this paper) but, unfortunately, investigators have rarely been very specific or precise in their measurement and description of environmental conditions. Nevertheless, a summary of the reported conditions should

serve to characterize the microhabitats in which Campe-  
loma are found. This summary provides the background  
information necessary for a study such as the present  
one, which aims at analyzing the nature of the influence  
of certain environmental factors on the movements and  
distribution of the snails. Together, the two bodies of  
information describe where the snails are found and why  
they are found there.

The following refers only to lotic populations of  
Campeloma. They are usually found in shallow water,  
anywhere from a few centimeters to a meter in depth.  
Although they have been collected from logs, mud or algae  
covered rocks, and masses of submerged vegetation along  
banks, they are usually found buried in penetrable  
substrates. These include sand, mud, muck, gravel, clay,  
and silt, with and without organic material, alone and in  
various combinations, and in various particle size  
ranges. Current velocities have been described as  
anything from quiet to swift or rapid; from zero to fifty  
centimeters per second. In the few instances in which  
current has actually been measured rather than qualita-  
tively described, measurements were taken at or near the  
water-air interface, yielding higher values than those  
prevalent at and especially in the substrate. This is  
evident in several cases in which a fine, easily eroded  
substrate and a high current velocity estimation are

given for the same microhabitat description. At any rate, both the typical microhabitat and the majority of microhabitats are described as having low current velocities. Campeloma have been found in waters of surprisingly low total alkalinity, with a reported range of 7 to 159 parts per million calcium carbonate. The ranges of other chemical parameters reported for Campeloma habitats include pH 5.68 to 8.5, dissolved oxygen concentrations from 8.6 to 10.8 parts per million, and carbon dioxide concentrations of 0 to 25.75 parts per million. The habitats of lotic Campeloma, then, are characteristically in shallow water with a soft substrate which the snails can penetrate, a slow current (at least at the bottom), and have any of a broad range of chemical conditions.

#### Summary of Studies on the Movements and Distribution of Campeloma

Having some knowledge of the relative importance of environmental factors in determining the distribution of Campeloma and some knowledge of the conditions which characterize their habitats, a study of their movements and consequential distributions becomes a productive possibility.

There have been only three published studies of more than passing concern with the distribution and movements of Campeloma in streams. Shelford (1914) undertook one

of the earliest laboratory stream studies on the reactions of freshwater animals to environmental factors. One of these animals was Campeloma subsolidum. Allison (1942), a parasitologist, published a brief report on the use of dung for baiting Campeloma spp. Included in this report was an account of the movement of the snails in a stream section as revealed by a mark and recapture method using chicken dung bait traps. Bovbjerg (1952) conducted a fairly thorough study of the distribution and movements of Campeloma decisum under natural and semi-natural stream conditions. Each of these studies has an important bearing on the present study.

Shelford (1914) collected his specimens from an Illinois creek and tested them within one week of collection. He characterized Campeloma subsolidum as a member of the pool community. Tests determining reactions to current were made in an "Allee Straight Current" artificial stream apparatus. This is a recirculating device provided with an incandescent light source and used at three velocities; 4-6 cm/sec, 10-12 cm/sec, and 16-20 cm/sec. Five individuals were used in nearly all tests. They were placed in the center of the stream and allowed time for adjustment before readings were taken (30 minutes in the case of Campeloma). The orientation of a snail was designated positive if it was headed upstream, negative if it was headed downstream, and for both cases

it had to be within about 16 degrees of the direction of the current. Those showing any other orientation were counted as indefinite. Those withdrawn in their shells or washed against a screen at the downstream end were counted as inactive or out of the experiment. The substrate was simply the bare floor of the stream device. The results for the tests on C. subsolidum were as follows: in the 4 to 6 cm/sec current velocity range, 50% of all snails showed a positive orientation, 10% negative, 30% indifferent, and 10% no activity, 90% of the snails were active and of these, 55% showed a positive orientation, 10% negative, and 35% indifferent; in the 10 to 12 cm/sec current velocity range, 80% of all snails showed a positive orientation and 20% showed no activity; in the 16 to 20 cm/sec current velocity range, 10% of all snails showed a positive orientation and the rest, 90%, showed no activity.

Shelford also tested reaction to substrate type. The tests were conducted in two metal pans, containing one or two centimeters of standing water, under controlled light and temperature conditions. The bottom of one pan was covered with wax, half of the bottom of the other with sand, and the other half with wax containing quartz dust to provide a surface resembling stone. He did not specify how or where the Campeloma were placed. He found that Campeloma "after creeping about for some

time in the unnatural conditions of the experiment, come to rest, burrow in the sand, in most cases with a small portion of the body protruding". All of the Campeloma tested burrowed in the sand.

A third kind of test conducted by Shelford was for reactions to light. Campeloma were tested for response to a light gradient but showed no activity. He obtained no other results concerning the relations of Campeloma with light.

Allison (1942) published a report describing a technique for trapping Campeloma through the use of dung as bait. Most of the report is concerned with details of this technique but Allison includes an account of a brief experiment he conducted on the movements of the snails. The experiment and its results are summarized in the following quotation:

It was suspected that in streams the current might carry the fecal extract which the snails followed to its source at the trap. This idea was tested by planting marked snails at various distances, two to 15 feet, upstream, as far as 20 feet downstream, and ten feet across the stream from a trap. In collections made at weekly intervals for five weeks, 23 of the 67 snails (41.7 per cent.) planted upstream, 24 of the 86 (26.7 per cent.) planted downstream, and 2 of the 9 (22.2 per cent.) planted across the stream were taken at the trap. Practically the same number of snails moved to the trap from 15 feet upstream and 20 feet downstream as from 2 feet up- and downstream. My data indicate that the snails move at random.

These results are clearly relevant to the present study.



Bovbjerg (1952) published a study on "ecological aspects of dispersal of the snail Campeloma decisum". This was a field investigation with experiments conducted under natural and semi-natural conditions. The stream, Dickerson Creek, is similar to Mill Creek, from which collections were made for the present study, and is in a neighboring county. The same species is the subject of both studies. Bovbjerg's study provides a good field-work counterpart to my laboratory stream study and each makes largely distinct contributions to a fuller understanding of the influence of environmental factors on the movements and distribution of Campeloma.

Bovbjerg made population density estimates at several transects along a section of the stream. Once he had established the general pattern of distribution of the snails in the stream section under investigation, and noted that aggregations occurred downstream from barriers to upstream movement, Bovbjerg conducted experiments to investigate the reactions of Campeloma to current and to physical barriers.

For the first series of these experiments he placed a wooden flume seventeen meters long and twenty centimeters wide on the stream bed. "The bottom was covered with sand and gravel simulating natural physical conditions" and contained about ten centimeters of water.

"Rate of current was regulated by partial blocking or funneling at the upstream end." Current velocity was measured by timing a float. For each experiment, 100 marked snails were placed at the midpoint of the flume and recaptured after 24 hours. "One set of 6 replicate experiments was conducted with a mean rate of current approximating 25 cm./sec., corresponding roughly to that of the adjacent stream. A second set of 6 experiments was performed at near 5 cm./sec. mean rate; such a slow rate is characteristic of only the most quiet reaches of the stream." Bovbjerg's results are presented in Table

1. Of the 600 snails tested at the higher current

Table 1. The distribution of snails within the experimental chute after a 24-hour period. Numbers are totals of 6 replicate experiments involving 100 snails each at 25 cm./sec. and 6 at 5 cm./sec. The release point was at 0. The direction of water flow was from left to right. (from Bovbjerg, 1952)

Meters	8	7	6	5	4	3	2	1	0	1	2	3	4	5	6	7	8	
25 cm./sec.	122	125	18	17	34	71	49	55	21	35	21	10	4	6	6	3	1	2
5 cm./sec.	181	126	72	23	23	40	24	13	25	18	5	11	10	16	5	2	6	0

velocity, 512 and a mean of 85.33 showed positive rheotaxis and 88 with a mean of 14.67 showed negative rheotaxis. At the lower velocity, the corresponding numbers are 527 with a mean of 87.83 and 73 with a mean of 12.17. There is little difference in the snails' movements at the two velocities except that at 5 cm./sec. there were 402 snails above 5 meters upstream compared to only 282 at

25 cm./sec. This is indicative of a greater rate of movement at the lower velocity.

Since the flume had a slope matching that of the stream, Bovbjerg conducted an experiment with gravity as the variable rather than current velocity to determine what influence gravity might have. The following is his description of the experiment and the results obtained:

A shorter, 4-meter chute of similar construction was placed at right angles to the stream axis. Current was eliminated. Eight replicate sets of 40 snails were tested by the release-recapture techniques previously described. One-half of these were tested with the chute level, the other half in the chute with a drop of 10 cm. in 4 meters.

In both level and tilted chutes the percentage dispersing towards the two ends was essentially equal. In each case approximately 50 per cent remained within one-half meter of the release point; the remaining snails were equally distributed in the two ends of the chute. The tendency was apparently to move randomly near the release point with but a few wandering to the ends of the chute. The trails left in the sand tend to support this view. The subjective impression was of less movement than in flowing water.

Thus Bovbjerg found that; 1) the directional movement observed in the first set of experiments represented a rheotactic rather than a geotactic response; 2) movement in still water was essentially at random; and 3) movement is less extensive in still water than in moving water.

The next experiment conducted by Bovbjerg involved fully natural conditions. He released 500 marked snails "in a characteristic reach of the stream" and every 24

hours for six days he sampled transects at five meter intervals upstream and downstream from the point of release. Snails found were returned in the same position to the stream. "The foremost marked specimen moved upstream at the rate of approximately 10 meters per day" and only one was found downstream. "On successive days the median snail was 0, 5, 10, 10, 15 and 15 meters upstream of the release-point". Thus there was nearly total upstream movement under natural conditions at the time and place of the experiment. The rate of movement was 2.5 meters per day for the median snail.

The last two experiments conducted by Bovbjerg were a pair of duplicates using the flume. These experiments were designed to investigate the reactions of the snails to a barrier to upstream movement.

Water in the upstream third of the previously described chute was impounded by a small obstruction of stones; this created a miniature pond, rapids, and flowing stream. Depth of the ponded water was 15 cm. and that of the flowing water 5 cm. with a 10 cm. drop.

In each of the 12 one-meter segments below the obstruction, 10 marked snails were dispersed uniformly. These were recaptured and their positions recorded at 24, 48, and 72 hours.

The results, which appear in Table 2, show continuous and nearly total upstream movement to the barrier. At the end of 72 hours, 110 of the 120 snails tested in the first experiment and 114 of the 120 tested in the second were located within one meter downstream of the barrier.

Table 2. Duplicate experiments demonstrating the reaction to a small barrier of stones at meter 6 of the experimental chute. Numbers are snails recovered on 3 successive days. A total of 120 snails were tested in each experiment. The direction of water flow was from left to right. (from Bovbjerg, 1952)

Meters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	
0 hr.	0	0	0	0	0	0	10	10	10	10	10	10	10	10	10	10	10	
24 hr.	0	0	0	0	0	0	40	48	8	5	5	4	3	2	0	2	3	0
48 hr.	0	0	0	0	0	0	86	28	1	1	0	3	0	0	0	0	1	0
72 hr.	0	2	0	0	0	0	110	2	3	0	1	1	0	0	0	0	1	0
0 hr.	0	0	0	0	0	0	10	10	10	10	10	10	10	10	10	10	10	10
24 hr.	0	0	0	0	0	0	66	12	8	6	9	6	5	5	0	3	0	0
48 hr.	0	0	0	0	0	0	92	6	5	3	3	5	4	0	1	1	0	0
72 hr.	2	0	0	0	0	0	114	0	2	0	1	0	0	0	1	0	0	0

In each of the duplicate experiments, two snails managed to traverse the barrier and continued to move upstream.

#### Objectives of the Present Study and its Place in the Literature

The primary objective of the present study is to determine what influence different levels of current velocity, substrate type, and light have on the movements and consequent distributions of Campeloma decisum in small streams. The preceding discussion on the known and probable influences of various environmental factors on the distribution of stream benthos indicates the

primary importance of current velocity, substrate type, and food supply. Other investigators of the movements of Campeloma have not compared movements in the light or day with those in the dark or at night. Shelford (1914), in his artificial stream study, applied three well-defined levels of current velocity but only one substrate type. Allison (1942) provided no clear indication of current or substrate conditions in the stream section he used for tests. Bovbjerg (1952) provided only vague description of substrate conditions in his field experiments. He specifies two levels of current velocity (three including still water) but used values obtained by timing a float over a measured distance, a method which yields a poor approximation of actual velocities at the stream bed. Artificial stream devices such as that which I used lend themselves to the application of numerous levels of current velocity, substrate type, and light conditions. The controlled conditions of an artificial stream study provide a powerful analysis of the influence of environmental factors on the behavior of an animal, free from the confusing complexity of natural conditions. It is for these reasons that I chose to conduct an artificial stream study on the movements of Campeloma and to utilize current velocity, substrate type, and light condition as variable factors.

A major drawback of artificial stream studies is their lack of realism in reference to nature. Discussion of the behavior of Campeloma based strictly on my laboratory test runs would be limited to the experimental conditions applied. Any extension to natural stream situations is dangerously speculative. Thus, to obtain the fullest possible degree of understanding of the influence of these factors on the snails, I have used my own results as the basis for a discussion which, along with the artificial stream study of Shelford (1914), draws upon the complimentary natural and semi-natural stream studies of Allison (1942) and Bovbjerg (1952). In addition, I have drawn upon other studies on the biology and ecology of Campeloma and on the behavior of other aquatic animals in relation to current, substrate, and light in search of a much more complete understanding than could be drawn from my investigations alone. It is my intention that such an approach will make the present paper more meaningful than it would otherwise be.

A corollary objective is to elucidate the rheotactic responses of Campeloma. A controversy has developed in the literature on this topic. Allison (1942) found that "the snails move at random". Bovbjerg (1952), however, concluded that the snails exhibit "a positive upstream movement". Thus it has remained uncertain whether or not positive rheotaxis is a characteristic response of

Campeloma. More accurately, it has remained uncertain which sets of environmental conditions elicit the response of positive rheotaxis and which elicit the response of negative rheotaxis or no rheotaxis at all. The present study was designed to yield results which might reconcile these opposed conclusions and combine them, with the aid of the rest of the literature, into a more comprehensive understanding of rheotaxis in Campeloma.

Numerous other lesser objectives are entailed in the above. The burrowing habit of Campeloma is unique among freshwater gastropods. I hope to discover what influence substrate type, and light have on the ability and tendency of the snails to burrow. I hope also to learn of any responses which appear to be substitutions or replacements for the burrowing response under conditions in which burrowing is impossible. When movement, rather than burrowing, occurs, the rate and path of movement is of interest as well as the overall direction (upstream or downstream). Another objective is to investigate what influence light, current velocity, and, especially, the presence or absence of physical obstacles in the form of substrate have on the rate of movement and path of the snails.



## THE BIOLOGY AND ECOLOGY OF CAMPELOMA

### Introduction

This section on the biology and ecology of Campeloma is intended to impart a fundamental understanding of the biology of an organism as a prerequisite for analyzing and explaining the behavior of that organism. The relative obscurity of Campeloma decisum and the many peculiarities of its biology (especially the lack of males in northern species, the taxonomic problems, ovoviviparity, and the burrowing habit) make this necessary for understanding my discussion of results obtained and the conclusions reached.

### General Biology of Campeloma

#### Taxonomy, classification of genus (Taylor and Schl, 1962)

Phylum Mollusca

Class Gastropoda

Subclass Streptoneura

Order Mesogastropoda

Superfamily Viviparacea

Family Viviparidae

Genus Campeloma

Taxonomy, Michigan species

Goodrich (1932) lists five species of Campeloma for Michigan. These are C. decisum (Say), which will be described in detail, C. integrum (Say), more slender than decisum and having more rounded whorls, C. milesi (Lea), even more slender, C. rufum (Haldeman), having a reddish hue noticeable in the aperture and at the apex, and C. subsolidum (Anthony), a heavy form. In addition, two subspecies are listed. These are the ventricose C. rufum gibbum and the stout, thick C. integrum obesum.

Taxonomy, identification of specimens as C. decisum

The species identification of the specimens used in the tests was determined to be Campeloma decisum on these bases: 1) The characteristics of the shell and the visible body conform most closely to those of C. decisum as described by F. C. Baker (1928a) which remains the most thorough and detailed key. The taxonomic keys and descriptions of Goodrich (1932), Goodrich (1944), and Harman and Berg (1971) corroborate this identification. 2) The radulae of six of the test snails were extracted and examined. They corresponded favorably with F. C. Baker's (1928) illustrations and description of the radula of C. decisum. 3) C. decisum is the most common, widespread species in Michigan (van der Schalie, personal

communication). C. integrum is believed to be a more western species by F. C. Baker (1928a), and Goodrich (1944) states that this species "has never been convincingly separated from C. decisum". C. milesi is described as "closely related to decisum" by F. C. Baker (1928a). Goodrich (1932) believes that it may be a mutation of C. decisum and indicates that C. rufum is a lake form although it has been taken from streams. According to Goodrich (1932), C. subsolidum occurs in Michigan only in the southwestern corner. It is closely related to C. integrum (Baker, F. C., 1928a) and may be an ecological variation of C. integrum or C. decisum (Goodrich, 1944). Thus, of the species attributed to Michigan, the specimens collected are most likely to be C. decisum and most properly given that name. 4) The snails were collected from Mill Creek in Kent County. Campeloma collected by Bovbjerg (1952) in neighboring Montcalm County were identified as C. decisum by H. van der Schalie. Both creeks are tributaries of the Grand River.

#### Taxonomy, taxonomic difficulties with the genus

As the preceding discussion indicates, there is considerable confusion and difficulty in the taxonomy of the genus Campeloma. Clench (1962) states in reference to Campeloma: "On a specific level, probably few genera

among our North American freshwater mollusks are in a more confused state. The answer to this condition is fairly simple, as there are but few morphological characters upon which specific differentiation can be made and these few characters differ only in degree." Specific differences are often established on the basis of characteristics which cannot be verified by measurement and no specific differences in the soft parts have been found (Goodrich, 1944). The problem becomes even more difficult when it is realized that, so far as is known, all Campeloma occurring as far north as Michigan reproduce parthenogenetically (Anderson, 1966; Chamberlain, 1958; Mattox, 1938; Medcof, 1940; Van Cleave and Altringer, 1937; and van der Schalie, 1965). The standard species criterion of interbreeding to produce fertile offspring does not apply to parthenogenetically reproducing groups. Since the specimens used for the test runs most nearly fit the characteristics given for Campeloma decisum, and since species names have been and continue to be applied to members of this genus, the test snails will be classified and referred to as C. decisum in the present study. However, use will be made of information concerning other species, especially that information which is generally applicable to the genus as a whole. Also, it is to be expected that much of what is stated in the present study concerning C. decisum will

hold for the other northern species as well. This is reasonable in view of the fact that the taxonomic difficulties are based on a lack of meaningful differences among the species.

Anatomy, shell and operculum

A brief description of the shell of Campeloma decisum may be found in many of the numerous appropriate keys. Several authors have provided more detailed descriptions, the most detailed being that of F. C. Baker (1928a), which is summarized here. The shell is elongate-ovate, subfusiform, and thin. Its color is dark green through olive to brown. There are six flatly rounded whorls, all of which are covered with brown, revolving, epidermal striae. The spire is long and pointed, sharply conic, with a flat-topped apex which, along with the upper whorls, is usually eroded. The sutures are deep. The aperture is elongately-ovate, rounded below and acutely angled above. The columellar wall of the aperture is covered by a brown-bordered callus which is tightly appressed to the parietal wall. The shell is either completely imperforate or has a very small chink. The thick, horny operculum fits the aperture snugly. The markings on it are entirely concentric or subconcentric, with the nucleus situated a little below center near the columellar margin. There are

usually four or five dark rest marks at regular intervals on the operculum.

Anatomy, external anatomy of body

According to F. C. Baker (1928a), Campeloma decisum, like other members of the genus, has a very large foot. It extends beyond the rostrum and covers a larger area than the shell. The foot is rounded behind and squarely truncated in front with auriculated corners. The head is small and the rostrum short and narrow. The eyes are on peduncles at the outer margins of the bases of the narrow, tapering tentacles. In males, the right tentacle is modified to form a penis sheath. The body is generally yellowish, the foot lead colored, and the rostrum and tentacles bluish. The head, tentacles, and upper surface of the foot are thickly spotted with orange.

Anatomy, internal anatomy

The internal anatomy of C. decisum will not be treated in detail here. The radula and genitalia are well described by F. C. Baker (1928a). The reproductive system and various other internal structures have been described by several authors but the study of Call (1886b) on the anatomy of C. subsolidum remains the most complete account for the genus. Excellent illustrations of the gross anatomy of male and female C. ponderosum coarctatum

are to be found in a paper by van der Schalie (1965). In Campeloma, the mouth and buccal mass, which contains the radula, are within the rostrum. The whorls above the body whorl contain the stomach, heart, and gonads. The single gill or ctenidium, with afferent and efferent gill veins, extends from the heart to near the edge of the mantle, in the body whorl. The renal opening and rectum are located on the right, dorsal surface of the mantle, near the edge. At a similar location on the left side is the osphradium. I have not found any description of the nervous system pertaining specifically to members of this genus.

#### Life history, reproduction

It is probable that all northern forms of Campeloma, which includes all colonies of C. decisum, lack males and reproduce parthenogenetically (van der Schalie, 1965; Anderson, 1966). Out of 450 C. decisum examined, Medcof (1940) failed to find a single male and concluded that parthenogenesis was the normal form of reproduction for the colony studied. Chamberlain (1958) found no males among over 800 C. decisum examined. I also have found only female Campeloma in all collections made in Michigan, including the 48 test snails. In Campeloma, the sexes are distinguished by the shape and size of the tentacles (Chamberlain, 1958). The right tentacle of

males is a sheath for the penis and is shorter and wider than the left. In females, both tentacles are long and thin. Chamberlain (1958) found only the stages of meiosis up to anaphase of the first division among C. decisum. He found two metaphase stages in oogonial division, each with 24 to 26 chromosomes. In parthenogenetic reproduction by Campeloma, chiasma formation occurs and is followed by reduction in chromosome numbers (van der Schalie, 1965). The normal diploid number is restored by the fusion of nuclei.

#### Life history, embryology

The most thorough study of uterine young in this genus is that of Van Cleave and Altringer (1937) on C. rufum. They found that the shells of the uterine young range in height from about 1.5 mm to 4.5 mm. The lower limit for gravid individuals is about 20 mm in shell height. Most gravid snails contained around 50 young. The uterine young are more uniform in size and greater in number in the fall and winter than during the parturition period of May through September. The period required for embryonic development is estimated to be about nine months. Mattox (1938) reports that during most of the year, the uterus of C. rufum contains stages varying from early veliger larvae to embryos 4 mm in shell height. Anderson (1966) studied Campeloma of undesignated species



collected in Ohio. She found that her specimens could be placed into categories of shell height according to the number of uterine young they contained. No snails under 20 mm contained uterine young. Those from 20 mm to 30 mm contained early stage larvae and, rarely, a few well-developed young. The largest number of well-developed young were found among those snails between 30 and 35 mm in shell height. Those over 35 mm contained few or no uterine young.

#### Life history, birth

All the Viviparidae are described by van der Schalie (1936) as being ovoviviparous. The young hatch from the eggs before they are expelled from the parent. It is hypothesized that ovoviviparity provides some advantage to the young in facing an unfavorable environment and for this reason has survival value. Crabb (1929) has observed the process of birth in Campeloma decisum. He believes that the "egg membrane is ruptured either by the young snail before being extruded or by the process of extrusion". This membrane is quite delicate and ruptures readily. According to F. C. Baker (1918a), the young of C. decisum are born in the spring. Chamberlain (1958) found that parturition in C. decisum occurs from mid-March until the end of June, with the most active period being late March through early April. The size of

the uterine young is not the sole stimulus for parturition and it doesn't appear to be related to water temperature. His specimens were collected in North Carolina. Van Cleave and Altringer (1937), working with C. rufum collected in Illinois, report that parturition is most active in May but occurs until the end of August. Young are present in the uterus throughout the fall and winter but none are released until the spring.

Life history, growth and development

The colony of Campeloma rufum studied by Van Cleave and Altringer (1937) had a mode of shell height of 4 mm at birth in May, 12 mm by September, and 20 mm by the following May. Thus they begin to bear young at the age of one year. Individuals at two years of age have a mode of 30 mm. Few individuals above 30 mm are gravid and most of these die in the fall or winter although some snails are gravid up to the maximum size of 40 mm. Bovbjerg (1952) found a similar tri-modal distribution of shell height (new born, one year, two years) for C. decisum in a Michigan colony. Sizes were smaller among the C. decisum collected by Chamberlain (1958) in North Carolina. The modes of shell height were 3 mm at birth in March, 8 mm by October, and 10 mm by the age of one year. At two years, which was the age of sexual maturity, the snails averaged over 15 mm in shell height. A

mode of 17 to 20 mm represented the third year. Medcof (1940) collected 55 C. decisum from the Speed River of Ontario. Of these, the one year olds were 5 to 12 mm in shell height with 0% gravid. At age two, they ranged from 13 to 18 mm and 18% were gravid. At age three, they were 19 to 23 mm and 77% were gravid. The four year olds ranged from 24 to 28 mm in shell height and 93% were gravid. In comparing his results with those of Van Cleave and Altringer (1937), he concluded that the Ontario colony of C. decisum grows more slowly, reaches sexual maturity later (age three), and lives longer (five years) than the Illinois colony of C. rufum.

#### Ecology of Campeloma

##### Range

The range of the genus Campeloma includes the eastern United States and southern Canada (Baker, F. C., 1928a). C. decisum has a distribution from Nova Scotia to Saskatchewan and south as far as Virginia through Tennessee, according to F. C. Baker (1928a). It has been reported from as far north as Ontario (Medcof, 1940) and as far south as North Carolina (Chamberlain, 1958). Harman and Berg (1971) describe the range of C. decisum as being "an area delimited by Nova Scotia and eastern Ontario south to Virginia".

## Dispersal

"Migration through the water is a major means of natural dispersal for all freshwater mollusks and it is the only important means for the gill-breathing prosobranch snails" (Harman and Berg, 1970). The Prosobranchia tend to be heavier, slower moving, and less able to withstand exposure to air than the Pulmonata and thus have a slower rate of dispersal (Harman and Berg, 1971). The most important means of dispersal for prosobranch snails such as Campeloma may be through gradual upstream movement. Long distance dispersal by Campeloma may be coupled with the slow process of base-leveling (Adams, 1901). This snail is better described as a quiet-water form than a rapid-water form (see Table 3). In the process of baseleveling, quiet-water conditions gradually extend upstream from the mouth as the stream gradient decreases through erosion. The quiet-water fauna, then, extends its distribution in the upstream direction in conjunction with the extension of quiet-water conditions.

## Burrowing habit

Snails of the genus Campeloma live buried, often completely, in mud or sand substrates (Allison, 1942; Clench, 1962; van der Schalie, 1965). C. decisum, in

particular, is described as a burrowing snail (Baker, F. C., 1911; Baker, H. B., 1922; Harman, 1972; Harman and Berg, 1971). This species is often found buried in mud or sand in both streams and lakes (Dawley, 1947; Medcof, 1940) and collections are usually made by sifting bottom materials (Allison, 1942; Bovbjerg, 1952; Shoemaker, 1961).

#### Habitats and microhabitats reported for Campeloma

Numerous authors have reported some characteristics of the habitats and microhabitats in which they have found Campeloma. This literature is presented in summary form in Table 3. This compilation provides an indication of the biotic and abiotic conditions which are favorable to Campeloma and it provides some indication of the range of conditions which the snails can tolerate. Since these authors have sampled a wide variety of habitats and microhabitats, the compilation is strong evidence (although of necessity not proof) that these are the only conditions under which populations of Campeloma will be found in nature.

#### Lake and stream variations

Morphological differences, especially in the shell, often exist between Campeloma living in streams and those living in lakes (Goodrich and van der Schalie, 1939).

Table 3. Some habitat and microhabitat conditions reported for Campeloma.

Source	<u>Campeloma</u> species	Habitat and microhabitat conditions reported
Allison, 1942	entire genus	streams; shallow water in mud
Anderson, 1966	unspeci- fied	river; in gravel or sand, at the base of willows or imme- diately downstream from rocks and logs
Baker, F. C., 1911	<u>decisum</u>	lake; shallow water, exposed and protected sandy shores river; in sandy mud, shallow water along shore, swift current river; surface of floating logs, on the lee side of anchored logs creek; buried in clean, firm sand, water a few inches to 2 or 3 feet deep, swift current, clear water
Baker, F. C., 1916	<u>decisum</u>	creek; pool, water from 1 to 2 or 3 feet deep, current slow, in very fine mud
	<u>integrum</u>	river; bordering bank, water

Table 3. Some habitat and microhabitat conditions reported for Campeloma (continued).

Source	<u>Campeloma</u> species	Habitat and microhabitat conditions reported
		from 1 to 3 feet deep, emergent aquatic plants, in mud or sand
	<u>decisum</u>	pond; water 6 to 8 feet deep, in mud
Baker, F. C., 1918a	<u>decisum</u>	lake; in sand and clay, more abundant in clay, 1.5 to 5 feet deep
Baker, F. C., 1918b	<u>decisum</u>	lake; in sand, water 1.5 to 3 feet deep, 6 snails in 2288 square inches sampled
		lake; in clay, water 2 to 5 feet deep, 10 snails in 1408 square inches sampled
		lake; in sand, water 2.5 feet deep, 1 snail in 32 square inches sampled
Baker, F. C., 1924	<u>rufum</u>	lake; in sand and mud, 3.73 per square meter
		river; water 30 to 50 cm deep, 31.24 per square meter
Baker, F. C., 1926	<u>rufum</u>	brook; in mud or sand, water

Table 3. Some habitat and microhabitat conditions reported for Campeloma (continued).

Source	<u>Campeloma</u> species	Habitat and microhabitat conditions reported
		shallow, vegetation, cold, clear water
Baker, F. C., 1927	<u>milesii</u>	lake; sheltered bay, in sand, water 1 to 2 feet deep, snails common
		lake; small protected bay, in soft mud near edge of water, water a few inches to a foot deep, <u>Chara</u> present, snails very abundant
		lake; bay, in sand, water a few inches deep, <u>Chara</u> present, snails abundant
Baker, F. C., 1928a	<u>decisum</u>	river; sand bars, buried in sand, water a foot deep, rapid current
		creek; in rocky-sandy bottom, shallow water
		creek; near mouth, in sand, shallow water
	<u>milesii</u>	river; wide and lake-like, in sandy-mud near shore,



Table 3. Some habitat and microhabitat conditions reported for Campeloma (continued).

Source	<u>Campeloma</u> species	Habitat and microhabitat conditions reported
		water a few inches to a foot deep, among aquatic plants
	<u>integrum</u>	river; in mud near shore, shallow water
	<u>rufum</u>	river; in sand, water 50 cm deep
		river; in mud, water 2.1 m deep
		river; in sand near shore, shallow water
		lake; in sand, water 30 to 80 cm deep
		lake; in mud, water 90 cm deep, vegetation present
		lake; in mud, water 1.2 m deep
		lake; in sandy mud, water 1 m deep
		lake; on boulder bottom, water 50 cm deep
		lake; in sand near shore, shallow water

Table 3. Some habitat and microhabitat conditions reported for Campeloma (continued).

Source	<u>Campeloma</u> species	Habitat and microhabitat conditions reported
		lake; in sand near shore, shallow water
	<u>brevi-</u> <u>spirum</u>	lake; in firm sand from shore to water 1 m deep, quiet water
		lake; widening of a creek, in mud, very shallow water, quiet water
		creek; below dam, on stones with slight covering of mud, shallow water, quiet water
Baker, H. B., 1922	<u>decisum</u>	lake; near shore, sand covered by thin layer of muck composed of bark, twigs, and other organic material, water-soaked logs, snails quite common
		lake; along shore near outlet, in muck held by dense bed of <u>Valisneria</u> , perceptible current, water more than one foot deep,

Table 3. Some habitat and microhabitat conditions reported for Campeloma (continued).

Source	<u>Campeloma</u> species	Habitat and microhabitat conditions reported
		snails quite abundant
		lake; in marly muck, water 2 or 3 feet deep, snails rare
		lake; in marly bottom, aquatic plants, water-soaked logs, water very turbid from sewage, snails very infre- quent
		creek; in sandy and mucky bottom, muck composed of decaying twigs and leaves, current not very swift, snails quite common
		river; below dam, in sandy clay along shore, water 4 to 12 inches deep, swift cur- rent, snails very common
		river; fine gravel with sand, some slight deposits of organic material, water about one foot deep, little vegetation, current not very

Table 3. Some habitat and microhabitat conditions reported for Campeloma (continued).

Source	<u>Campeloma</u> species	Habitat and microhabitat conditions reported
		swift, water with slight reddish tinge, snails common river; partially buried in small pockets of sand among rocks near shore, rocks coated with finely-divided deposit containing iron, snails common river; rapids above and below falls with backwaters of little current along the shore below the falls, snails rare
Bovbjerg, 1962	<u>decisum</u>	creek; coarse gravel and sand, silted margins, clear. well aerated, relatively unpolluted water, maximal current about 50 cm/sec, highest densities in margin- al areas of less current and with silt and detritus

Table 3. Some habitat and microhabitat conditions reported for Campeloma (continued).

Source	<u>Campeloma</u> species	Habitat and microhabitat conditions reported
		present
Call, 1886a	entire genus	ponds; in muddy bottoms streams; still flowing portions
Chamberlain, 1958	<u>decisum</u>	lake; in mud, water about 1 m deep lake; half-buried in a clayey silt with some sand and decaying organic debris, near shore
Clench, 1962	entire genus	lakes, rivers, and small streams; usually buried an inch or more in sand or mud
Dawley, 1947 <sup>4</sup>	<u>decisum</u>	rivers; small, width 10 to 50 feet, with pools and riffles rivers; medium sized, 50 to 100 feet wide, deep in center, with deep pools having sand or mud bottoms and shallow rapids having

Table 3. Some habitat and microhabitat conditions reported for Campeloma (continued).

Source	<u>Campeloma</u> species	Habitat and microhabitat conditions reported
		swift current and stony bottoms
		rivers; large, broad and deep, bordered by sandy beaches or marshes
		lake; soft water, total alkalinity about 35 ppm, sandy beaches
		rivers; river-lake, widening of river, more river than lake
		lake; river-lake, more lake than river but having a large river for inlet and outlet
		lakes and rivers; common in waters of low total alkalin- ity, often found buried in mud near river banks or sand near lake shores
Goodrich, 1932	<u>decisum</u>	rivers; favorite habitat is

Table 3. Some habitat and microhabitat conditions reported for Campeloma (continued).

Source	<u>Campeloma</u> species	Habitat and microhabitat conditions reported
		muck along river banks in slow-moving reaches, also found among weeds near banks in swift currents
Goodrich, 1944	entire genus	lakes and streams; typically in mud, slight current or wave-action
Harman, 1972	<u>decisum</u>	lakes and streams; in eulit- toral and littoral silt and detritus - fine organic and inorganic materials, normal- ly found in soft sand or organic substrates lake; under rotting logs in or near areas of sand bottom
Harman and Berg, 1971	<u>decisum</u>	lakes and streams; in soft substrate, quiet water, under edges of rotting logs, buried in silty substrates, water with pH from 7.3 to 8.5 with a mean of 7.9, dis- solved oxygen concentration

Table 3. Some habitat and microhabitat conditions reported for Campeloma (continued).

Source	<u>Campeloma</u> species	Habitat and microhabitat conditions reported
		from 8.6 to 10.8 ppm with a mean of 9.6, total carbon dioxide from 0 to 5 ppm with a mean of 2.8, and alkalinity as ppm calcium carbonate from 58 to 159 with a mean of 88 (total of 8 collection areas)
Medcof, 1940	<u>decisum</u>	pond; river mill pond, in soft black muck often smelling of hydrogen sulphide, from shore to a depth of 10 or 12 inches in summer, greater depths in winter river; below dam, on flat surface of rocks, in dense mat of <u>Cladophora</u>
Morrison, 1932	<u>decisum</u>	lakes and streams; pH from 5.68 to 8.37 and fixed carbon dioxide from 1.2 to 25.75 ppm
	<u>milesii</u>	lakes and streams; pH from



Table 3. Some habitat and microhabitat conditions reported for Campeloma (continued).

Source	<u>Campeloma</u> species	Habitat and microhabitat conditions reported
		5.86 to 8.0 and fixed carbon dioxide from 1.1 to 24.73 ppm
Schmid, personal communication	<u>decisum</u>	river; mostly in organic sand and bare sand, some in sandy gravel and gravel, current from 0 to 60 feet per minute, water from 2 to 24 inches deep
Shelford, 1914	<u>subsoli-</u> <u>dum</u>	streams; pools, usually in sand, occasionally in mud, rarely among vegetation
Shoemaker, 1961	<u>decisum</u>	creek; in mud
Shoup, 1943	<u>decisum</u>	streams; total alkalinity from 7 to 135 ppm calcium carbonate
	<u>lewisii</u>	streams; total alkalinity from 10 to 20 ppm calcium carbonate
	<u>pondero-</u> <u>sum</u>	streams; total alkalinity from 63 to 70 ppm calcium carbonate

Table 3. Some habitat and microhabitat conditions reported for Campeloma (continued).

Source	<u>Campeloma</u> species	Habitat and microhabitat conditions reported
van der Schalie, 1965	<u>pondero-</u> <u>sum co-</u> <u>arctatum</u>	creek; at mouth, in soft mud, water 1 to 4 feet deep
	entire genus	lakes and streams; in mud or sand

There is evidence that physiological and behavioral differences exist as well. F. C. Baker. (1928b) studied the fate of the molluscan fauna of a number of small creeks which were turned into lakes by the building of a dam. The Campeloma (C. decisum) either migrated upstream from the newly created lakes into the upper, unchanged reaches of the streams or perished in the new lakes. None successfully established themselves in the lakes even though there are well established lake variations of the same species in the same area. During the winter, C. decisum living in a hundred acre mill pond of the Speed River, Ontario, were found to be hibernating at some depth in the bottom mud whereas those living in an adjacent, flowing stretch of the river remained active, moving over the hard bottom (Medcof, 1940). In the summer, the water level in the pond fluctuates rapidly and often and the Campeloma move with the shoreline, thus

remaining at about the same water depth. They congregate in a band from the shore to a depth of about one foot. In sharp contrast, snails living in algal mats on rocks in the flowing river remained in the same positions for two days and appeared to have been there considerably longer.

#### Typical densities and aggregations

Typical population densities of Campeloma in lakes may range from 4 to 48 per square meter (Baker, F. C., 1918b). These densities are typical for most bottom areas where the snail is found. Aggregations of Campeloma in lake habitats are known to occur near rotting logs (Harman, 1972). In the pond situation described above, Medcof (1940) reports that "it is seldom more than an hour's work to collect 200 or 300" snails.

Bovbjerg (1952) did a thorough study of Campeloma population density in a section of a Michigan stream. He sampled five to nine quarter square meter quadrats in each of ten transects across the stream. At the first transect, 20 meters downstream from a dam, there were an average of 6 snails per quadrat. At the second transect, 40 meters below the dam and just below some rapids, there were 607 snails per quadrat. Densities steadily decreased below this peak in the successive downstream transects, which were spaced at 20 meters. At 60 meters

below the dam, the mean density was 297 snails per quadrat. At 80 meters, the mean was 147, 100 meters - 112, 120 meters - 67, 140 meters - 41, and 160 meters - 36. At about 200 meters downstream from the dam, just above a second rapids, there were only 3 snails per quadrat. Just below the same rapids the mean density jumped to 243 per quadrat. This is an illustration of some typical densities and of a type of aggregation peculiar to streams - immediately downstream from obstacles preventing upstream movement. Another kind of aggregation found in streams is that formed around decaying organic matter (Allison, 1942). I have observed aggregations of Campeloma around a dead crayfish and on a submersed and decaying log, both in a stream.

#### Feeding habits

F. C. Baker (1918b) describes Campeloma decisum as a herbivorous-detritus eater. It feeds on plants, detritus, and carrion with detritus including both animal and plant material in the water or deposited in the substrate. Allison (1942) and Shoemaker (1961) describe Campeloma as being coprophagous, so fecal material should be included among the food sources. Clench (1962) and Harman and Berg (1971) provide more recent confirmation of all these food sources for Campeloma.

C. decisum dissected within three hours of collection revealed mud in the first part of the intestine (Chamberlain, 1958). Later, mud was found only in the rectum as feces. After five hours the entire gut was empty. Young snails were kept in the laboratory for 15 months with only some decaying organic matter in a fine substrate for food. C. decisum appears to feed "by ingesting bottom materials containing decaying organic matter". Beyond this, details of feeding in Campeloma are not yet known. But van der Schalie (1965) speculates that "the relatively small size of the buccal mass as well as the long and thin esophagus indicates that the food would not be coarse particulate material". The anterior portion of the foot has extensive glandular and muscular development which suggests some unusual and highly specialized feeding mechanisms, especially in view of the small size of the stomach and digestive gland.

#### Parasites

Campeloma are commonly infested with metacercaria in the uterus. Medcof (1940) found as high an incidence of infestation as 88% in C. decisum. This trematode may be Leucochloridiomorpha constantiae (Chamberlain, 1958) or a new species, L. papillata, discovered by Shoemaker (1961) in C. decisum from Michigan. The adults may be found in ducks. Medcof (1940) reports a mite, identified as

Unionicola campelomaicola, living in the mantle cavity of Campeloma. He also found snails parasitized by the leech Helobdella nepheloidea. I have also observed leeches on C. decisum. The protozoan Ptychostomum campelomae is a parasite occurring in the intestine of Campeloma (Hyman, 1967).

### Predators

Pennak (1953) considers fish the greatest predators on snails and lists ducks, shore birds, amphibians, leeches, beetle larvae, Hemiptera nymphs, and Odonata nymphs as other predators. Leeches may be referred to as predatory but they are best described as parasites. Only the very young of Campeloma would be likely to fall prey to the other invertebrates. According to F. C. Baker (1918b), Campeloma are not fed upon by fish in New York State. Medcof (1940) examined the stomachs of nine bullfrogs and found that Campeloma formed about 24% of the contents. He also found three undigested Campeloma in freshly regurgitated pellets of the European starling.

### Coexistence with other mollusks

Populations of Campeloma are sometimes mixed with those of Viviparus or Lioplax or both at the same site (Van Cleave and Chambers, 1935; Van Cleave and Lederer, 1932). All three genera are members of the family

Viviparidae. I have found Campeloma buried in sandy stream bottoms in close association with fingernail clams and with Viviparus at the surface of the sand. Many gastropods, such as Pleurocera, Gyraulus, or several other species are often to be found on rocks, plants, or the bottom near Campeloma.

#### Pollution tolerance

Campeloma "respond rapidly and completely to essential modifications in environment" (Call, 1886a). These modifications can be brought about by thermal, organic, or inorganic pollution. They have been known to disappear from sections of streams receiving municipal or industrial wastes and they cannot tolerate temperatures much over 32° C. Most prosobranchs are considered typical of clean waters (Harman and Forney, 1970). Richardson (1928) describes the Viviparidae as "cleaner-water species", the category of least tolerance to pollution in his seven-category system.

## MATERIALS AND METHODS

### Location and Description of the Laboratory

The laboratory in which all research was conducted was located in the basement of an unoccupied house on the campus of Western Michigan University. This house was, at the time of the study, being used by the Department of Biology for research purposes. The basement is well suited for the operation of a small artificial stream.

### The Artificial Stream

#### General description of the arrangement

The artificial stream, or flume, itself was constructed of three-quarter inch exterior plywood. The floor and interior walls of the flume were coated with an epoxy enamel paint, light gray in color. The flume was supported on tables at a height of about 80 cm from the basement floor. It was level across the width with a uniform slope lengthwise.

Located on the floor, beneath the lower or outlet end of the flume, was the collecting pond. The collecting pond was a plastic wading pool, about 27 cm deep and 1.42 m in diameter with a capacity of about 427 l.

The pump used to circulate water through the system was a one-third horsepower Wayne submersible sump pump,



rated at 47 gallons per minute (178 liters per minute) at a discharge head of five feet (1.52 m). 1.5 inch (3.8 cm) PVC pipe was used with the pump.

The pump was situated against the wall of the collecting pond, beneath the overhanging lower end of the flume. It delivered the water through pipe running beneath the flume, over the upper end to a maximum height of 1 m, and down toward the floor of the intake area. The water then flowed downhill through the flume and dropped back into the collecting pond to be recirculated.

#### Overall dimensions of the flume

The flume was 3.05 m long, 76 cm wide, and 18 cm deep. The upper end of the flume was elevated 2 cm from the horizontal to provide a slope.

#### Divisions of the flume

The intake area occupied the full width of the flume and 28 cm of the length, starting at the upper end wall. It was bordered at its downstream end by a sheet of ordinary aluminum window screen, intended to help smooth the flow of water into the test area. Immediately downstream from the screen was the 10.5 cm high upper dam. This dam height was found to be the most effective in providing a uniform flow from the intake area.

The test area was 2.49 m long. Across the width of the floor near each end was a row of five uniformly spaced bolts. These were used to secure a moveable wall at any one of four settings which determined the effective width of the flume. A separate plastic dam of appropriate width was fitted between the moveable wall and the right wall (facing upstream) of the flume, just below the upper dam, to force the water through the effective test area at each width setting. The narrower the effective width, as determined by the position of the moveable wall, the faster the current velocity provided. The flume thus provided effective width settings of 76 cm (moveable wall removed), 58 cm, 46.5 cm, 35 cm, and 23 cm. The starting line used in all the tests was a line across the width of the flume at the middle of the test area, which was also the middle of the entire flume.

The outlet area had the same dimensions as the intake area. It was separated from the test area by a lower dam of adjustable height. The lower dam height used depended upon the substrate type in place for a test run. In this manner, an approximately equivalent water depth could be maintained over all substrate types used. The lower end of the flume was covered by another sheet of window screen to prevent large particles from falling into the collecting pond and entering the pump.

## Current Velocities Used

### Still water

For still water tests, the full width of the test area was used (76 cm). The test area was filled with water until it overflowed the lower dam. A maximal depth determined by the substrate type and lower dam height being used was maintained throughout the test run.

### Moderate

Moderate velocity was obtained by positioning the moveable wall to provide an effective test area width of 46.5 cm. Current velocity was measured with an A. Ott small current meter type 10 152 with a 30 mm diameter propeller, a stand, and a counter. Readings were taken at 12 points spaced 4 cm apart along the starting line, with the propeller as near the floor as possible. The average velocity along the starting line was thus determined to be 3 cm/sec, to the nearest cm/sec. At all settings of the moveable wall, the velocity increases slightly in the upstream direction and decreases in the downstream direction, especially as the region of back-wash caused by the lower dam is approached. But these changes are not great within 90 cm on either side of the starting line and very few of the snails even approached that distance during any of the tests. In

addition, it is the velocity at the starting line to which the snails are first exposed and react.

### Fast

The effective test area width yielding fast velocity is 23 cm. An average velocity along the starting line of 14 cm/sec was obtained from readings taken at 6 points spaced 4 cm apart, in the same fashion as for moderate velocity. Both current meter velocity determinations were checked against a modification of a formula (Needham and Needham, 1962) for velocity in which the velocity is approximately equal to the pump discharge divided by the cross sectional area for the appropriate flume setting. The two current meter velocity determinations proved to be reasonable both in absolute magnitude and relative to each other.

### Reasons for selection of current velocity settings used

The three current velocities selected from the range of possibilities provided by the flume apparatus were the slowest (still water), the fastest (fast), and the velocity most nearly intermediate between these extremes (moderate). These velocities were selected so that the snails could be tested under the full range of available velocity conditions without taking the cumbersome and complicated approach of using every velocity setting.

### Substrate Types Used

The substrate types were sorted from gravel pit gravel obtained in Kent County, Michigan. Some sand from an excavation site in Kalamazoo County was also used. The gravel and sand were hand sorted with sieves selected from the U. S. Standard Sieve Series, manufactured by the Dual Manufacturing Co., Chicago, Illinois. Six particle size categories were separated according to my modification of the widely used Wentworth classification (Wentworth, 1922). These are defined in Table 4. My modification is based on the recommendations of Cummins (1962) for the use of the Wentworth Scale by benthic ecologists. No particles in the boulder size range were collected. My substrate types cobble and pebble are identical with those of Cummins (1962). I divided gravel into coarse and fine, the former being impenetrable and the latter penetrable to Campeloma attempting burrowing. The sands, silt, and clay were lumped together for simplicity into coarse and fine sand. Most of the smaller particles in fine sand were removed by washing of the substrate. All six substrate types were thoroughly washed to remove the clay and silt. This was done to reduce water turbidity during test runs and to prevent organic silt, a possible food source for Campeloma, from becoming an unwanted additional variable.

Table 4. My substrate type classification and its relationship with the classifications of Wentworth (1922) and Cummins (1962).

Particle size range in mm	Wentworth classification	Cummins' modification	My modification
>256	boulder	boulder	boulder
64-256	cobble	cobble	cobble
32-64		pebble	pebble
16-32	pebble		
8-16			<u>coarse gravel</u>
4-8		gravel	fine gravel
2-4	<u>granule</u>		
1-2	very coarse sand	very coarse sand	coarse sand
0.5-1	<u>coarse sand</u>	<u>coarse sand</u>	
0.25-0.5	<u>medium sand</u>	<u>medium sand</u>	
0.125-0.5	<u>fine sand</u>	<u>fine sand</u>	
0.0625-0.125	very fine sand	very fine sand	fine sand
0.0039-0.00625	<u>silt</u>	<u>silt</u>	
<0.0039	clay	clay	

Two of the six substrate types sorted were used for test runs. These are coarse gravel and coarse sand. The third substrate type used in test runs was the bare floor of the flume. Coarse gravel presents a rugged, impenetrable surface to the snails and is more nearly typical

of microhabitats in which Campeloma has been found (see Table 3) than either cobble or pebble. Pilot tests showed that of the three penetrable substrate types; fine gravel, coarse sand, and fine sand; coarse sand was the substrate in which the snails most readily and quickly burrowed. Pilot tests also indicated that movement was much more extensive over the bare floor than over any other substrate. The three substrate types chosen, then, offered a sampling of the full range of likely responses by the snails; maximal rate and extent of movement on the floor, immediate burrowing in coarse sand, and the possibility of either shelter seeking or extensive movement over the rugged, impenetrable surface of coarse gravel. As a matter of convenience, coarse sand will henceforth be referred to simply as sand and coarse gravel as gravel.

#### Light Conditions Used

The light source for the artificial stream consisted of two florescent light fixtures situated 1.3 m above the stream floor and centered over its full length. Each unit contained four 40 watt tubes. Average light intensity at the stream floor was measured with a Weston Model 756 Illumination Meter and determined to be 105 foot candles.

Conditions of darkness approximating those of a shaded stream at night were obtained with the lights out by blacking out the windows of the laboratory area.

#### Collection and Preparation of Test Animals

##### Location of collection sites

All the snails tested were collected at sites within a five-meter-long section of Mill Creek, near the 8 Mile Road bridge, in Alpine Township, Kent County, Michigan. I had thoroughly sampled this stretch of Mill Creek in the summer of 1972 and was familiar with the microhabitats favored by Campeloma. This is a pool area and most of the bottom consists of sand mixed with silt.

##### Baiting technique

To facilitate the collection of an adequate number of snails, a modification of the baiting method for Campeloma first suggested by Allison (1942) was used. Acting on a suggestion that Campeloma may be coprophagous, Allison (1942) buried small cloth bags of chicken dung in stream locations frequented by these snails. Within a period of one to two weeks after planting the bait, he was able to collect the unusually large numbers of Campeloma crowded around it. I followed a similar procedure, substituting dog dung for chicken dung.



Before each of the three collections of test snails, one or two bait bags were shallowly buried at various points in the soft, silty sand bottom of the stream. An area was chosen in which Campeloma was known to be common. Bait was planted in this manner from 10 to 14 days before each of the collection dates of September 16, October 10, and November 2, 1973.

#### Collection technique

There was little variation in the positions of the bait bags. At each collection an aggregation of snails, often more than 20, was found within a 200 sq cm area around each bait bag. Only one or two would typically be found in the same area without bait. The snails were examined and their shell height estimated with a ruler. At least 16 individuals measuring between 2.0 and 2.5 cm in height were collected each time. A majority of the snails examined fell within this size range. Collected snails were placed in a large glass jar with stream water and substrate from the collection site and transported to the laboratory on the same day.

#### Marking of individuals

When the snails were brought to the laboratory, they were removed from the jar to a tray, washed, and individually marked. Each individual in a test group of eight

snails was marked with a Roman numeral (I, II, III, IV, V, VI, VII, or VIII) so that the movement of every individual could be observed and recorded separately. The marking was accomplished by scratching the body whorl of the shell with a nail. This removed the dark material encrusting the shell to reveal the more lightly colored layers beneath.

#### Acclimation period

After collection and marking, the two test groups were placed in separate holding tanks and left undisturbed for a period of from 16 to 38 hours to acclimate to laboratory conditions. This procedure was followed for each of the three test series.

#### Preparation and Maintenance of the Laboratory for Storage and Testing of the Snails

#### Holding tanks

The holding tanks were two 10 gallon aquaria situated side by side on a counter top in the laboratory. Each contained a 2 cm deep layer of a substrate composed of a mixture of equal parts of my substrate types fine sand, coarse sand, fine gravel, and coarse gravel. The snails can and do burrow into this substrate and it seemed sufficiently dissimilar from any one of the substrates used for test runs to avoid a possible source of bias in

the results. A water depth of about 5 cm over the substrate was maintained in each holding tank. Aeration was provided by two air stones, one located in the same corner of each tank, and both connected to a single air pump. The water was constantly aerated.

#### Addition of water to holding tanks and collecting pond

About two days before the start of each test series, water was added to the holding tanks and the collecting pond of the stream system. The collecting pond was emptied and refilled to the point of overflowing with fresh, cold tap water before each series.

#### 24 hour cycles of light and darkness

All the light fixtures in the laboratory were turned on and off automatically by a timing device set to approximate, within 15 minutes, the sunrise and sunset times existing at the start of a series. The timer was reset to the appropriate times before each succeeding test series. Thus the artificial daylength of the laboratory corresponded closely with the natural daylength at the time the test snails were collected.

#### Experimental Design

There are three categories of variables; substrate type, current velocity, and light condition. The three

substrate types and current velocities and the two light conditions were defined and described above. Various combinations of the variables in these three categories were applied in each of two half hour tests conducted daily, one at 12:30 PM and the other at 3:00 PM. Two groups of eight snails were used in one test apiece per day. The test times for each group were reversed daily so that both groups were tested the same number of times at 12:30 and at 3:00. This arrangement was intended to balance out any possible bias due to the time of day of testing. The variables were applied in all possible combinations so that a test series consisted of  $3 \times 3 \times 2$  or 18 tests for each group. The conditions of light and dark were reversed between the two daily test times every other day so that in every period of four consecutive days, beginning with day 1, each group experienced light once and dark once at each test time. The basic test schedule so far described is illustrated in Table 5. The current velocities and substrate types were scheduled into this basic test schedule in specific combinations determined by the use of a magic square, shown in Table 6. This procedure facilitates the application of an analysis of variance in that use of the magic square (so called because the sum of each row or column is equal to the same number, in this case 15) results in any point in

Table 5. The basic test schedule. The letters A and B represent snail groups A and B. The letters L and D represent light and dark, the two light conditions. Days 5 through 8, 9 through 12, and 13 through 16 repeat the pattern shown for days 1 through 4. Days 17 and 18 repeat the schedule for days 1 and 2.

Day	12:30	3:00
1	AL	BD
2	BL	AD
3	AD	BL
4	BD	AL
17	AL	BD
18	BL	AD

Table 6. The magic square.

Substrate type	Current velocity		
	Still	Moderate	Fast
floor	1	5	9
sand	6	7	2
gravel	8	3	4

the test schedule being equivalent, for statistical purposes, with any other point. The numbers indicate the order in which the 3X3 or 9 possible combinations of current velocity and substrate type were used. For each of the four combinations of snail group and light condition (for example, the AL, AD, BL, and BD of Table 5) a number was selected at random from the magic square and used as the starting point in an ordered sequence. The

random numbers obtained for series 1 were 6 for AL, 4 for AD, 7 for BL, and 5 for BD. As an example, the first time AL appears in the schedule it is assigned the number 6, representing the combination of still water and sand. The second time AL appears, it is assigned the number 7, the third time 8, and so on. Each number represents a specific combination of current velocity and substrate type as determined by the magic square (Table 6). The test schedule for series 1, generated in this manner, appears in Table 7.

#### Test Schedules

For series 2, in which groups C and D were tested, the random numbers obtained for starting points were 5 for CL, 8 for CD, 3 for DL, and 8 for DD. The test schedule generated appears in Table 8. For series 3, involving groups E and F, the starting points were 8 for EL, 5 for ED, 8 for FL, and 4 for FD. The resulting test schedule appears in Table 9.

#### Test Procedure

##### Preparation of the flume for tests

The moveable wall was not used in still water tests. For running water tests, it was positioned to provide the effective stream width yielding moderate or fast

Table 7. The test schedule for series 1. For each entry, the first letter (A or B) represents the group of snails, the second letter represents light (L) or dark (D), and the number represents the combination of current velocity and substrate type indicated by the same number in the magic square.

Day	Date	12:30	3:00
1	9-17-73	AL6	BD5
2	9-18-73	BL7	AD4
3	9-19-73	AD5	BL8
4	9-20-73	BD6	AL7
5	9-21-73	AL8	BD7
6	9-22-73	BL9	AD6
7	9-23-73	AD7	BL1
8	9-24-73	BD8	AL9
9	9-25-73	AL1	BD9
10	9-26-73	BL2	AD8
11	9-27-73	AD9	BL3
12	9-28-73	BD1	AL2
13	9-29-73	AL3	BD2
14	9-30-73	BL4	AD1
15	10-1-73	AD2	BL5
16	10-2-73	BD3	AL4
17	10-3-73	AL5	BD4
18	10-4-73	BL6	AD3

velocity. The lower dam height was adjusted to 5 cm for floor tests and to 7.5 cm for sand or gravel tests. This

Table 8. The test schedule for series 2, involving groups C and D. The second letters and the numbers in the entries have the same meanings as in Table 7.

Day	Date	12:30	3:00
1	10-11-73	CL5	DD8
2	10-12-73	DL3	CD8
3	10-13-73	CD9	DL4
4	10-14-73	DD9	CL6
5	10-15-73	CL7	DD1
6	10-16-73	DL5	CD1
7	10-17-73	CD2	DL6
8	10-18-73	DD2	CL3
9	10-19-73	CL9	DD3
10	10-20-73	DL7	CD3
11	10-21-73	CD4	DL8
12	10-22-73	DD4	CL1
13	10-23-73	CL2	DD5
14	10-24-73	DL9	CD5
15	10-25-73	CD6	DL1
16	10-26-73	DD6	CL3
17	10-27-73	CL4	DD7
18	10-28-73	DL2	CD7

assured that the water depth was about the same for all test runs, regardless of the substrate type in use. If sand or gravel were to be used, the material was poured into the test area and leveled. The amount of substrate



Table 9. The test schedule for series 3, involving groups E and F. The second letters and the numbers in the entries have the same meanings as in Table 7.

Day	Date	12:30	3:00
1	11-4-73	EL8	FD4
2	11-5-73	FL8	ED5
3	11-6-73	ED6	FL9
4	11-7-73	FD5	EL9
5	11-8-73	EL1	FD6
6	11-9-73	FL1	ED7
7	11-10-73	ED8	FL2
8	11-11-73	FD7	EL2
9	11-12-73	EL3	FD8
10	11-13-73	FL3	ED9
11	11-14-73	ED1	FL4
12	11-15-73	FD9	EL4
13	11-16-73	EL5	FD1
14	11-17-73	FL5	ED2
15	11-18-73	ED3	FL6
16	11-19-73	FD2	EL6
17	11-20-73	EL7	FD3
18	11-21-73	FL7	ED4

material added for a test was proportional to the effective width setting to be used so that the same thickness was present in tests run at all the velocity settings. When all these preparations had been made as necessary,

water was introduced to the flume and it was ready for the snails.

#### Positioning of the snails

The appropriate group of eight snails was removed from a holding tank and placed on a white enameled tray. The snails were arranged along a line across the width of the tray, facing alternately left and right. For each test, the sequence of marked individuals along the line was determined by random numbers corresponding to the numbers on the snails. They were then transferred to the starting line of the flume in the same pattern, with gaps of about 1 cm between them. The left-right pattern avoided the bias involved in pointing the snails upstream or downstream prior to beginning the test. Use of the random sequence assured that an individual was not always facing the same direction or occupying the same position, relative to other individuals, along the starting line. This eliminated the unconscious tendency to repeatedly place certain individuals in the same relative position, which is a possible source of bias.

#### Conduction of a test

Before the timing of a test run was begun the snails were allowed to extend and secure themselves to the substrate. This procedure was not actually necessary for

still water tests but in moving water tests, especially at fast velocity, the snails may be rolled downstream by the force of the current. Obviously, such movement is not voluntary on the part of the snails and cannot be recorded as distance traveled. This would be a particular problem in the case of tests run in the dark. For this reason, a test run was not begun until it was clear that all the snails were secure in their positions and capable of locomotion. Once it had been determined that the snails were ready, the appropriate conditions of water flow and/or darkness were established and timing of the test run was initiated. Tests being conducted under light conditions were checked occasionally to observe the movements of the snails. All test runs were one half hour in duration, the amount of time it took the swiftest snails to approach the upper or lower dams, moving over floor, in pilot tests. At the end of the half hour the pump was turned off and/or the lights on, as necessary. The snails' positions were immediately determined and recorded. A meter stick was used to measure the distance, to the nearest centimeter, from the center of the shell to the starting line along a line parallel to the sides of the flume. The group of snails was then returned to its holding tank.

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Purposes, Limitations, and Advantages of Artificial  
Stream Studies

Both laboratory and field studies have their advantages and limitations. The most thorough and comprehensive studies of behavior use both approaches (Savory, 1959). The movements of animals as observed under field conditions are influenced by a complex of environmental factors of varying importance. Data gathered from field observations and studies represent the total influence of this complex. It is the particular advantage of laboratory studies that these factors become isolated variables in a controlled situation and the relative importance of each can then be determined. Very often, conclusions drawn from field studies can be enhanced in terms of detail and accuracy, and thus gain considerable meaning, by the application of laboratory investigations. This should be done whenever it is practical to do so (Allee, 1913). The results of the present study, supplemented by the laboratory investigations of Shelford (1914), are considered along with the results obtained from the field observations and experiments of Allison (1942) and Bovbjerg (1952). This integrated approach provides a more comprehensive understanding of the behavior of Campeloma than that which would be provided by any of the component studies alone. Since Shelford's laboratory study was limited in scope and the work of Allison and

Bovbjerg was conducted under natural or semi-natural conditions, the present study was needed to provide this highly desirable comprehensiveness.

There have been few laboratory stream studies investigating the influence of environmental factors on the distribution of benthic stream invertebrates (Cummins, 1964). The distribution of freshwater mollusks has been correlated with environmental factors but there has been little experimental study of these correlations (Muirhead-Thomson, 1958). The macrohabitats and microhabitats in which Campeloma has been found have been described to varying degrees by a number of authors but only the present study and the three mentioned in the preceding paragraph have attempted experimental investigations of the behavior resulting in the observed distributions. The present study, then, fills a particular need in this area of ecology.

Probably the major limitation of artificial stream studies is their lack of reality. Because the streams used are artificial, many of the attributes of natural streams have been eliminated from them and the organisms are tested under conditions which differ from the reality of their natural habitats (Warren, 1971; Warren and Davis, 1971). The greatest value of natural studies is that the situation is real, not an abstraction from reality. The organisms are in their natural settings

(Carthy, 1958; Warren, 1971). The two kinds of study are complimentary. As mentioned earlier, they should both be used for a comprehensive investigation. Recirculating artificial streams, such as the one used in the present study, depart from the reality of nature especially in that they do not have the natural stream attribute of continuous downstream movement of all the water. The use of an artificial stream for a study should be geared to the objectives of the study. The interpretation of results from such a study is constrained by the ways in which the artificial stream is used. Any generalizations based on the results of an artificial stream study must be made only with extreme caution (Warren and Davis, 1971). In the present study I have sought to investigate the influence of current velocity, substrate type, and light on the movements and distribution of Campeloma. The materials and methods used were chosen and designed with this objective in mind. My results are fully applicable only under the conditions in which they were obtained. With care, however, the interpretation of these results can yield valuable insights into the behavior of the snails in nature. And, when interpreted in combination with the results from semi-artificial and natural studies on Campeloma, my results may be used with even greater confidence to generalize about the behavior of the snails. I have used this cautious and integrated

approach to formulate my conclusions. It is only by doing so that they can have their greatest value and most extensive meaning.

The major advantage of artificial stream studies is that the number of environmental variables can be reduced and the remaining controlled. This allows investigation of the response of the organisms to just a few or only one environmental factor (Thut, 1969). There are associated advantages of "conceptual focus, spatial limitation, simplification, control, manipulation, and measurement" (Warren and Davis, 1971). In its natural habitat, "the organism is confronted with many varying conditions; not often can we ascertain which of these, singly or together, are leading to the responses we observe. It is for this reason that so many studies of the individual organism are conducted in the laboratory" (Warren, 1971). A laboratory study allows the investigator to determine the influence of a few selected environmental factors on the movements of the individuals. It can be determined how the various factors act, which are the more important, and whether or not they interact in various combinations. This information can then be used to help explain the observed behavior of the organism under the complex conditions of a natural ecosystem.

A good artificial stream study should have certain attributes, these include the following: 1) the

conditions chosen for use should be made as relevant as possible to the problems under investigation; 2) the study should be designed so that it is capable of providing truly meaningful insights, not merely incidental information; and 3) the artificial stream system "should be the simplest that can incorporate the circumstances leading to the phenomena we seek to understand", the strength of laboratory studies resides in their simplicity (Warren and Davis, 1971). It was with these desirable attributes in mind that I designed and conducted the present study.

Artificial streams used for autecological studies can be simpler than those used for synecological studies (Warren and Davis, 1971). The influence of abiotic factors on the movements of an organism can be more readily studied in an artificial stream than the influence of biotic factors (Warren, 1971). An artificial stream system offering organisms a selection of abiotic conditions can be used to determine their preferred habitats (Warren and Davis, 1971). The present study was an autecological investigation involving the influence of certain abiotic factors on the movements of Campeloma. Although the snails were not offered a selection of substrates, current velocities, or light intensities in tests I conducted, differences in their behavior with changes in each of these factors reveals much about



habitat selection by Campeloma. Thus the present study takes advantage of many of the more useful aspects and possibilities of artificial stream studies.

One additional advantage of artificial stream studies, and an important purpose, is the following:

In laboratory studies, we learn how particular environmental factors and combinations of factors influence some of the responses of the individual organism that determine the distribution and abundance of its population. This provides another basis for predicting the effects of environmental change, a basis that is not limited by the historic range of environmental conditions. For this reason, laboratory studies are particularly valuable as one basis for predicting the effects of man's activities on the distribution and abundance of populations (Warren, 1971).

## RESULTS

### Raw Data

The data obtained from test runs were in the form of centimeters moved upstream or downstream from the starting line by each snail in every test. To distinguish between the two directions, values for movement upstream were recorded as positive and values for movement downstream were recorded as negative. Snails at the starting line were recorded as zero. Date, time, and test conditions, along with water temperature, were recorded for each test run.

### Treatment of the Raw Data

#### Terminal location

The raw data were treated in three ways for the application of an analysis of variance. The first is terminal location. In this treatment, the means were obtained from the algebraic sums of distances moved (algebraic sums of the raw data). This is a direct approach to the raw data and provides an index to the direction and extent of movement simultaneously.

Terminal distance

The second treatment is terminal distance. The means for this treatment were obtained from the sums of the absolute values of the distances moved. The positive and negative signs, and thus the direction of movement, are ignored. This provides an index to the extent of movement alone. It's an indication of the relative ability and tendency of the snails to move.

Percentages moving upstream, downstream, and not moving

The third treatment has three parts; the percentages of individuals moving upstream, downstream, and not moving. The mean percentages were obtained from the sums of the percentages of tested individuals with terminal locations at the starting line, upstream from it, or downstream from it. Corresponding mean percentages for the three parts of this treatment always sum to 100% and are most useful when considered in combination. Extent of movement is disregarded altogether and direction of movement is expressed as mean percentages of individuals taking a direction rather than mean centimeters moved in a direction. The use of all three of these treatments rather than something less provides a maximal advantage in interpreting the data. Each contributes to an understanding of the results.

## Comparison of the Levels of Each Factor

### Groups

The initial application of an analysis of variance to the raw data was for a comparison of the levels of each variable environmental factor. Means were compared between groups within each series and among the three series as well as for the three current velocities, three substrate types, and two light conditions. In each case, these comparisons were made using all the treatments.

There are no significant differences, with F at the 5% level, between the means for the two groups in any of the series, by any treatment. Thus the data for both groups in each series can justifiably be combined for purposes of comparing the series.

### Series or time of year

With the exception of one treatment, terminal distance, this is also the case for the three series, as shown in Table 10. There is a significant difference among the means of 11.2 cm for series 1, 8.0 cm for series 2, and 12.0 cm for series 3 in the terminal distance treatment. This treatment is an indication of the extent of movement. The significant difference presents a problem in justifiably combining data from all three series. However, the differences among the means

Table 10. Comparison of the means among the three series by each treatment.

Treatment	Value of F. <sub>.05,2,42</sub>	Significant differences (F. <sub>.05,2,42</sub> =3.22)	Level (Series)	Mean
terminal location	0.109	no	1 2 3	0.9 cm 1.7 cm 1.1 cm
terminal distance	8.079	yes	1 2 3	11.2 cm 8.0 cm 12.0 cm
percentage upstream	1.584	no	1 2 3	31.3% 34.7% 33.5%
percentage downstream	0.154	no	1 2 3	34.7% 35.1% 33.3%
percentage not moving	1.175	no	1 2 3	34.0% 30.2% 28.1%

for the terminal distance treatment, although significant, are not exceedingly great, especially between series 1 and series 3 which are furthest apart in time. And the terminal location treatment, which provides an index to the extent and direction of movement simultaneously, and the three-part third treatment, which is

concerned only with the direction of movement, both lack any significant differences among their means. For these reasons, it was decided that the results for all the series could be combined and considered as a single experiment. There was little difference in the observed behavior of the snails from series to series. This was also true from month to month during the period of the study, since series 1 took place mostly in September, series 2 in October, and series 3 in November, 1973.

#### Current velocity

Current velocity proved to be a significant factor in the terminal distance, percentage moving upstream, and percentage not moving treatments, as shown in Table 11. The extent of movement was similar at moderate and fast velocities but significantly less in still water. Terminal location was increasingly far in the upstream direction with increasing current velocity, although the differences are not great enough to be significant. However, significantly greater percentages of individuals moved in the upstream direction with increasing current velocity. This was at the expense of the percentages not moving since there are no significant differences among the percentages moving downstream at the three velocities.

Table 11. Comparison of the means among the three current velocities by each treatment.

Treatment	Value of $F_{.05,2,94}$	Significant differences ( $F_{.05,2,94}=3.10$ )	Level (Velocity)	Mean
terminal location	2.610	no	still moderate fast	-0.9 cm 1.8 cm 2.8 cm
terminal distance	16.342	yes	still moderate fast	7.9 cm 11.6 cm 11.7 cm
percentage upstream	4.493	yes	still moderate fast	29.9% 34.0% 40.6%
percentage downstream	0.087	no	still moderate fast	33.7% 34.4% 35.1%
percentage not moving	8.472	yes	still moderate fast	36.5% 31.6% 24.3%

#### Substrate type

The great importance of substrate type as an environmental factor influencing movement is indicated by significant differences in the means for floor, sand, and gravel in every treatment (Table 12). In all respects,

Table 12. Comparison of the means among the three substrate types by each treatment.

Treatment	Value of F.05,2,94	Significant differences (F.05,2,94=3.10)	Level (Substrate type)	Mean
terminal location	3.991	yes	floor	4.2 cm
			sand	-0.1 cm
			gravel	-0.5 cm
terminal distance	366.851	yes	floor	29.0 cm
			sand	0.6 cm
			gravel	1.6 cm
percentage upstream	29.624	yes	floor	53.5%
			sand	24.0%
			gravel	27.1%
percentage downstream	11.388	yes	floor	44.4%
			sand	25.7%
			gravel	33.0%
percentage not moving	131.566	yes	floor	2.1%
			sand	50.4%
			gravel	39.9%

the difference between movement on sand and on gravel was minor compared with the difference between movement on either and movement on the floor. The extent of movement was immensely greater on floor than on sand or gravel. Terminal location was 4.2 cm upstream on the floor but within a centimeter of the starting line on sand and



gravel. A much greater percentage of individuals moved both upstream and downstream on floor than on sand or gravel because only 2.1% failed to move on floor while 39.9% failed to move on gravel and 50.4% failed to move on sand.

#### Light condition

The means for the two light conditions are significantly different in the terminal distance, percentage moving upstream, and percentage not moving treatments, as indicated in Table 13. Movement was significantly more extensive in the light than in the dark. The terminal location was 1.6 cm further upstream in the light than in the dark but this difference is not significant. There was a significantly greater percentage of individuals moving upstream in the light than in the dark, however, and at the expense of the percentages not moving since there is no significant difference between the percentages moving downstream under each condition.

#### Significance of the Interactions of the Factors

##### Substrate type - current velocity interaction

It is clear that significantly great changes in the movement of the snails can take place with a change in the level of current velocity, substrate type, or light

Table 13. Comparison of the means between the two light conditions by each treatment.

Treatment	Value of $F_{.05,1,47}$	Significant differences ( $F_{.05,1,47}=4.05$ )	Level (Light condition)	Mean
terminal	1.564	no	light	2.0 cm
location			dark	0.4 cm
terminal	21.411	yes	light	11.9 cm
distance			dark	8.9 cm
percentage	16.722	yes	light	41.0%
upstream			dark	28.7%
percentage	0.177	no	light	34.9%
downstream			dark	33.8%
percentage	22.269	yes	light	24.1%
not moving			dark	37.5%

condition being applied. But these three environmental variables were not independently applied in a test, they were applied in unison. Therefore it is possible that they interacted in their effects on the snails. That is, the change in movement exhibited in going from one level to another of a variable factor may depend to a significant degree upon which level of one or both of the other variable factors is in effect simultaneously. The analysis of variance was also applied to discover in which treatments combinations of any two or all three of the variable factors showed significant interaction.

The first combination examined, substrate type and current velocity, appears in Table 14. There was significant interaction between these two factors in all treatments except percentage not moving. Thus there was significant interaction in terms of extent of movement, distance moved in a direction, and percentage of individuals moving in either direction.

Table 14. Significance of the interaction between substrate type and current velocity by treatment.

Treatment	Value of F <sub>.05,4,188</sub>	Significant interaction (F <sub>.05,4,188</sub> =2.42)
terminal location	2.694	yes
terminal distance	13.809	yes
percentage upstream	2.698	yes
percentage downstream	5.728	yes
percentage not moving	2.301	no

Light condition - current velocity interaction

Light condition and current velocity interacted significantly in all treatments except percentage moving upstream, as shown in Table 15. Again there was significant interaction in terms of both absolute and directional extent of movement. The two factors had no modifying influence upon one another in the case of the percentage of individuals moving upstream but they did

interact in causing individuals to move downstream or to fail to move.

Table 15. Significance of the interaction between light condition and current velocity by treatment.

Treatment	Value of F.05,2,94	Significant interaction (F.05,2,94=3.10)
terminal location	7.449	yes
terminal distance	21.411	yes
percentage upstream	0.680	no
percentage downstream	3.237	yes
percentage not moving	5.690	yes

Light condition - substrate type interaction

Light condition and substrate type also interacted significantly in all treatments but one. As Table 16 reveals, there was significant interaction in terms of extent of movement and of the percentages of individuals taking a direction or not moving but not in the case of the distance moved in a direction.

Light condition - substrate type - current velocity interaction

The significance of the interactions of all three factors is indicated in Table 17. This three-way interaction is significant in the treatments indicating extent of movement and distance moved in a direction. But in

terms of percentages of individuals, there was a significant interaction only in the percentage moving downstream treatment.

Table 16. Significance of the interaction between light condition and substrate type by treatment.

Treatment	Value of $F_{.05,2,94}$	Significant interaction ( $F_{.05,2,94}=3.10$ )
terminal location	1.356	no
terminal distance	14.322	yes
percentage upstream	3.643	yes
percentage downstream	4.492	yes
percentage not moving	7.130	yes

Table 17. Significance of the interaction among light condition, substrate type, and current velocity by treatment.

Treatment	Value of $F_{.05,4,188}$	Significant interaction ( $F_{.05,4,188}=2.42$ )
terminal location	9.302	yes
terminal distance	4.295	yes
percentage upstream	1.825	no
percentage downstream	3.925	yes
percentage not moving	1.351	no

## Comparison of Means for all Combinations of Levels of Factors

### Introduction

Substrate type, current velocity, and light condition all have significant effects on the movements of the snails. This was found to be the case for each factor with results from all levels of the other two factors averaged together. The three factors interacted significantly in all possible combinations. For these reasons, it is important to make a more thorough breakdown and analysis of the results. Such a breakdown, in which a mean is determined for movement in every combination of substrate type, current velocity, and light condition, appears in Table 18. This approach makes it possible to determine the influence of every level of each variable environmental factor on the movement of the snails, under every combination of conditions used, and for each treatment. Means for movement on floor, which was much more extensive than on sand or gravel, were compared for significant differences by use of either Student's *t* distribution or the analysis of variance. This information is also presented in Table 18.

### Movement on sand

It is immediately evident that movement over sand

Table 18. Means, by treatment, for all combinations of light condition, substrate type, and current velocity including the range and standard deviation, respectively, for the terminal location and terminal distance treatments and comparisons between means for movement over floor ( $t_{.05,94}=1.66$ ,  $F_{.05,1,47}=4.05$ ).

	Floor			Sand			Gravel		
	Terminal location								
Light Still	-1.9cm <sup>a</sup>	118	29.6	0.0cm	4	0.8	-0.7cm	27	3.9
Dark	-2.5cm <sup>b</sup>	136	26.9	0.1cm	3	0.5	-0.3cm	16	2.2
Light Moderate	18.4cm <sup>c</sup>	152	42.9	-0.3cm	3	0.9	-0.8cm	22	3.8
Dark	-6.6cm <sup>d</sup>	142	29.9	-0.1cm	11	1.6	-0.1cm	16	1.8
Light Fast	3.2cm <sup>e</sup>	146	39.0	0.1cm	3	0.8	0.3cm	15	2.5
Dark	14.8cm <sup>f</sup>	124	32.8	-0.3cm	4	0.9	-1.3cm	19	3.0
	Terminal distance								
Light Still	24.4cm <sup>g</sup>	57	16.5	0.6cm	2	0.6	2.2cm	17	3.3
Dark	19.0cm <sup>h</sup>	73	19.0	0.3cm	2	0.5	0.8cm	14	2.0
Light Moderate	41.4cm <sup>i</sup>	89	20.8	0.7cm	2	0.6	2.4cm	14	3.0
Dark	24.0cm <sup>j</sup>	78	18.7	0.7cm	10	1.5	0.7cm	9	1.7
Light Fast	33.4cm <sup>k</sup>	82	19.9	0.6cm	2	0.6	1.8cm	8	1.8
Dark	32.1cm <sup>l</sup>	65	15.7	0.7cm	3	0.7	1.6cm	17	2.8
	Percentage upstream								
Light Still	52.1% <sup>m</sup>			27.1%			35.4%		
Dark	27.1% <sup>n</sup>			18.8%			18.8%		
Light Moderate	64.6% <sup>o</sup>			20.8%			31.3%		
Dark	41.7% <sup>p</sup>			29.2%			16.7%		

Table 18. Means, by treatment, for all combinations of light condition, substrate type, and current velocity including the range and standard deviation, respectively, for the terminal location and terminal distance treatments and comparisons between means for movement over floor ( $t_{.05,94}=1.66$ ,  $F_{.05,1,47}=4.05$ ) (continued).

	Floor	Sand	Gravel
Percentage upstream			
Light	66.7% <sup>q</sup>	27.1%	43.8%
Fast			
Dark	68.8% <sup>r</sup>	20.8%	16.7%
Percentage downstream			
Light	47.9% <sup>s</sup>	25.0%	33.3%
Still			
Dark	66.7% <sup>t</sup>	6.3%	22.9%
Light	33.3% <sup>u</sup>	41.7%	41.7%
Moderate			
Dark	54.2% <sup>v</sup>	16.7%	18.8%
Light	33.3% <sup>w</sup>	22.9%	35.4%
Fast			
Dark	31.3% <sup>x</sup>	41.7%	45.8%
Percentage not moving			
Light	0.0% <sup>y</sup>	47.9%	31.3%
Still			
Dark	6.3% <sup>z</sup>	75.0%	58.3%
Light	2.1% <sup>aa</sup>	37.5%	27.1%
Moderate			
Dark	4.2% <sup>bb</sup>	54.2%	64.6%
Light	0.0% <sup>cc</sup>	50.0%	20.8%
Fast			
Dark	0.0% <sup>dd</sup>	37.5%	37.5%



Table 18. Means, by treatment, for all combinations of light condition, substrate type, and current velocity including the range and standard deviation, respectively, for the terminal location and terminal distance treatments and comparisons between means for movement over floor ( $t_{.05,94}=1.66$ ,  $F_{.05,1,47}=4.05$ ) (continued).

Means tested	Value of t or F	Significant difference	Means tested	Value of t or F	Significant difference
a,b	F= 0.013	no	a,c	t= 3.836	yes
a,e	t= 0.980	no	b,d	t=-0.975	no
b,f	t= 4.212	yes	c,d	F=11.530	yes
c,e	t=-2.856	yes	d,f	t= 5.186	yes
e,f	F= 3.176	no	g,h	F= 2.615	no
g,i	t= 6.492	yes	g,k	t= 3.426	yes
h,j	t= 2.084	yes	h,l	t= 5.420	yes
i,j	F=18.786	yes	i,k	t=-3.066	yes
j,l	t= 3.336	yes	k,l	F= 0.119	no
m,n	F= 6.714	yes	m,o	t= 1.787	yes
m,q	t= 2.085	yes	n,p	t= 2.102	yes
n,r	t= 6.007	yes	o,p	F= 5.785	yes
o,q	t= 0.298	no	p,r	t= 3.905	yes
q,r	F= 0.052	no	s,t	F= 3.721	no
s,u	t=-2.089	yes	s,w	t=-2.089	yes
t,v	t=-1.754	yes	t,x	t=-4.971	yes
u,v	F= 4.094	yes	u,w	t= 0.000	no
v,x	t=-3.217	yes	w,x	F= 0.052	no
y,z	F= 3.133	no	y,aa	t= 1.732	yes
y,cc	t= 0.000	no	z,bb	t=-0.778	no

Table 18. Means, by treatment, for all combinations of light condition, substrate type, and current velocity including the range and standard deviation, respectively, for the terminal location and terminal distance treatments and comparisons between means for movement over floor ( $t_{.05,94}=1.66$ ,  $F_{.05,1,47}=4.05$ ) (continued).

Means tested	Value of t or F	Significant difference	Means tested	Value of t or F	Significant difference
z,dd	$t=-2.334$	yes	aa,bb	$F= 0.329$	no
aa,cc	$t=-1.732$	yes	bb,dd	$t=-1.556$	no
cc,dd	$F=-----$	no			

was negligible. The extent of movement, as indicated in the terminal distance treatment, Table 18, in all cases averaged only a fraction of a centimeter. The one most universally consistent reaction of the snails observed was their tendency to burrow into sand, within a centimeter of their starting positions, and regardless of current velocity or light conditions. At the start of a test run with sand, the snails typically began burrowing at their starting positions and by the end of the test period were partially or completely covered. Some may have moved as much as a centimeter or two upstream or downstream in the process of burrowing, but there was no directional movement of any greater consequence than this throughout a test period. Therefore, differences in the movements of the snails over sand in various conditions

of current velocity and light are not of biological or behavioral significance although in some cases they are statistically significant.

#### Movement on gravel

Movement on gravel was more extensive than on sand and somewhat different in certain aspects of directional movement. With terminal distance means ranging from 0.7 cm to 2.4 cm, movement on gravel was at least reasonably measurable. In nearly every case, fewer individuals failed to move from the starting line on gravel than on sand and occasionally a snail traveled several centimeters. However, movement on gravel was still not sufficiently extensive to permit meaningful comparisons of movement under different conditions of current velocity and light. As for sand, the differences are not of biological or behavioral significance because the extent of movement was too slight. This becomes quite obvious when the extent of movement on either sand or gravel is compared with that on floor. Gravel is impenetrable to Campeloma so burrowing did not occur. The lack of extensive movement on gravel was due to the common tendency of the snails to move into crevices or pockets among the stones near their starting positions and remain in such areas for the duration of the test.

### Movement on floor

As mentioned above, movement on floor was much more common and extensive than on either sand or gravel and sufficiently so to make comparisons between the means obtained under the various combinations of current velocity and light conditions worthwhile and meaningful. Only the results of tests using this substrate yield useful information on the influence of current velocity and light on the movement of the snails. To facilitate comparisons of the means for movement on the floor, Table 18 includes determinations of statistically significant differences between pairs of these means.

The results for movement in still water can be summarized as follows: Movement was slightly more extensive in the light than in the dark but the difference is not significant. Directional movement averaged less than 3 cm from the starting line for both light and dark conditions. Significantly more individuals moved upstream in the light than in the dark. Nearly the same number of individuals moved upstream as moved downstream in the light but over twice as many moved downstream than upstream in the dark.

In moderate velocity, movement was significantly more extensive in the light than in the dark. Movement in the light and in the dark at moderate velocity was

significantly more extensive than in the light and dark, respectively, in still water. Directional movement was far upstream in the light (18.4 cm) and slightly downstream in the dark (-6.6 cm). Directional movement in the dark at moderate velocity is not significantly different from that in the dark in still water. Nearly twice as many individuals moved upstream as downstream in the light but a similar percentage moved in each direction in the dark.

Movement in fast velocity was almost equally extensive in light and in dark, there is no significant difference. It was significantly less extensive in light than in light in moderate velocity and significantly more extensive in dark than in the dark in moderate velocity. Also, movement in fast velocity was significantly more extensive in both light and dark than in still water. Directional movement was only slightly upstream in the light (3.2 cm) but strongly upstream in the dark (14.8 cm). In both light and dark, more than twice as many individuals moved upstream as moved downstream. At all three velocities, the percentage of individuals not moving on floor was either very small (6.3% at most) or zero.

Comparison of Results with Those of Shelford (1914),  
Allison (1942), and Bovbjerg (1952)

Shelford (1914)

Shelford's and the present study are the only to use an experimental artificial stream approach to factors influencing the distribution of Campeloma. The present study goes considerably further than Shelford's in investigating the effects of current, substrate, and light. The most important difference is that Shelford was concerned only with orientation in response to current whereas I was concerned with the direction, rate, and extent of movement. A comparison of results in respect to current is nevertheless beneficial. At 4 to 6 cm/sec, Shelford found 50% positive orientation, 10% negative, and 40% indifferent or no activity. At moderate velocity (about 8 cm/sec) and conditions of light and floor, I found 64.6% upstream, 33.3% downstream, and 2.1% not moving. There is no great difference in the percentages showing positive orientation or moving upstream but in the present study much fewer snails were indifferent or inactive and many more moved downstream than showed that orientation in Shelford's study. Of course, many of the snails which Shelford reports as having an indifferent orientation might eventually have taken an upstream or downstream direction. In moving up to the 10 to 12

cm/sec velocity, Shelford's results show 80% of the snails active and all these taking a positive orientation. An increase in current velocity brought about a more strongly positive rheotactic response. In the present study, at fast velocity (14 cm/sec) on floor and in the light, 66.7% of the snails moved upstream and 33.3% moved downstream with none failing to move. This set of results is only slightly different from that which I obtained for moderate velocity. In the present study, an increase in velocity from moderate to fast brought about only a slightly more positive rheotactic response. At the highest velocity used by Shelford, 16 to 20 cm/sec, 90% of the snails showed no activity. This is a reversal of the trend from his lowest to his intermediate velocities and opposite from the results at my highest velocity. Apparently, the snails tested by Shelford could do no more than maintain their positions at 16 to 20 cm/sec. But this seems unlikely or, if so, unusual because the snails I tested could and did orient and move in a current of 14 cm/sec. In general, the comparable results for response to current in the two studies are similar - positive rheotaxis was exhibited by 50% or more of the snails tested at velocities from 4 to 14 cm/sec.

The results pertaining to substrate type are in close agreement in that Campeloma in both studies tended to burrow in sand. Sand was the only penetrable

substrate type available to the snails in Shelford's study. He did not define the particle size range. It was also the only penetrable substrate used in the present study. In still or moving water in the present study nearly all of the snails burrowed in sand at or near their starting positions. Although Shelford did not test for substrate selection in moving water, the same results obtained for Campeloma in still water should be expected.

Both the current and substrate reaction tests conducted by Shelford were done in the light only. His study makes no contribution toward understanding the effect of the absence of light on the orientation and movements of Campeloma. This is one of my reasons for doing light and dark tests. Shelford's light gradient test involving Campeloma had no useful results.

#### Allison (1942)

Allison's experiment was conducted in a natural stream setting. The only artificial manipulations were the use of the dung bait trap and the planting of the snails. Once planted, the snails were free to move wherever they might and the bait was a close simulation of a common natural occurrence. This, then, was a study of the movements of Campeloma under natural conditions as opposed to the artificial stream approach of Shelford



and the present study. It was, however, a single and rather brief study for which there is an almost complete lack of reported information on substrate type and current velocity conditions in the study area. Also, Allison made collections at weekly intervals, taking no heed of possible changes in movement corresponding to daily or hourly changes in stream conditions or of movement in the light versus movement in the dark.

These shortcomings lessen the value of Allison's experiment but his conclusion, that the snails move at random, is nevertheless of great import to the present study. In moving water, whether at moderate or fast velocity, the movement over floor of the snails I tested was directional, predominantly upstream or downstream, and cannot be described as random. For still water, however, I obtained results which support Allison's conclusion. Although snails on the floor moved an average of 19.0 cm in the dark and 24.4 cm in the light, their mean terminal location was within 3 cm of the starting line. With the absence of a current there was no favored direction of movement. Movement was essentially at random in still water tests. This leads me to believe that Allison conducted his experiment within a stream pool, a macrohabitat in which current velocities tend to be minimal and in which there was probably a fine substrate suitable for burying the bait used. Indeed,

such a substrate is found only in areas of lower current velocity. A quiet water habitat is just the type of habitat described by Allison when he suggests that bait traps be placed in areas where the snails are commonly found. Allison's results, then, have important implications concerning the influence of current velocity, substrate type, and food supply on the movements and distribution of Campeloma. His experiment thus has important implications for the present study.

#### Bovbjerg (1952)

Bovbjerg made use of both natural and semi-artificial stream situations. Both Bovbjerg and I conducted experiments with the Campeloma contained in a flume. The obvious difference in the conditions of these experiments is that Bovbjerg's were conducted under manipulated but largely natural conditions with little control over the variables whereas mine were conducted under closely controlled artificial conditions. Both approaches have their advantages and disadvantages and, as mentioned earlier, compliment each other.

In Bovbjerg's first set of experiments, reaction to current was tested in a flume placed on the stream bed. Comparisons between substrate and current conditions in this flume and that used in the present study are made difficult by Bovbjerg's ambiguity. He describes his

substrate as "sand and gravel simulating natural physical conditions". There is no indication of the size range of particles, relative percentages of sand and gravel size particles, uniformity of distribution in the flume, or the amount and distribution of detritus. He observed some snails burrowing but it's not possible to obtain a good idea of how readily they could or did burrow at any given time or place in these experiments. I would estimate that his substrate more nearly resembled a combination of the sand and gravel substrate types of the present study than either sand or gravel alone. Bovbjerg used current velocities of 5 cm/sec and 25 cm/sec. The lower velocity is near the 8 cm/sec moderate velocity I used and the higher velocity is greater than my fast velocity of 14 cm/sec. However, Bovbjerg determined the velocities in his flume by timing the movement of a float. This method will tend to yield higher values for velocity than those prevalent just above the substrate, where current has its impact on the snails. In addition, current velocity in a small stream, as a function of discharge, may vary considerably in a 24-hour period. Therefore a direct comparison of velocities used in the two studies is not very reliable. Bovbjerg made no observations which allowed comparison between movement in the light and in the dark. This is one of the primary reasons that light was used as a variable in the present study. All of

these drawbacks and limitations to comparison must be kept in mind as precautions in relating Bovbjerg's study to the present study.

Bovbjerg's semi-artificial stream experiment results indicate predominantly positive rheotaxis at both velocities. At 5 cm/sec, 87.8% of the snails moved upstream and 12.2% moved downstream. At 25 cm/sec, 85.3% moved upstream and 14.7% moved downstream. On floor, at moderate velocity in the light and fast velocity in the light and dark, I found from 64.6% to 68.8% moving upstream and from 31.3% to 33.3% moving downstream. On floor, at moderate velocity in the dark, 41.7% moved upstream and 54.2% moved downstream. Thus Bovbjerg found that positive rheotaxis prevailed over negative in the ratio of 6 or 7 to 1, regardless of velocity. My results are in general agreement but with a lower ratio, 2 to 1 regardless of velocity, and with the exception of moderate in the dark. Bovbjerg obtained lower rates of movement than I found over floor. The movement over sand or gravel which I observed is too slight for such comparisons. Bovbjerg's results and those of the present study both indicate that the rate of movement, in light, decreases with an increase in current velocity from one non-zero value to another.

Bovbjerg used another semi-artificial stream for testing reaction to gravity in still water. The

conditions resemble those of the still water, light tests of the present study and the results are in general agreement. My flume was more nearly level than Bovbjerg's tilted chute position. He found that movement in still water was approximately equal toward both ends, regardless on whether the chute was level or tilted. In still water, on floor, I found 52.1% moving in the upstream direction and 47.9% moving in the downstream direction. His results indicate that movement is less extensive in still than in moving water, a finding supported by my results as well. Thus both studies indicate that movement of Campeloma in still water tends to be slower or less extensive and non-directional relative to movement in flowing water. These results have important implications for the consideration of Allison's conclusion that Campeloma move at random in streams.

Bovbjerg's release and recapture experiment was conducted under fully natural conditions. The results corroborate the strong positive rheotaxis found in the semi-artificial flume experiments. Little more than this can be said. The environmental conditions, including current velocity and substrate type, are unspecified and the habitat is described merely as "a characteristic reach of the stream". However, although undescribed and probably not measured, these are natural conditions at a

selected place and period of time and thus the results can be taken as representative of the movements of the snails in a natural habitat. But to say very much at all about the influence of current, substrate, and other factors on the movements of the snails requires a better understanding of the nature of these factors. Once again, no investigation was made of the influence of light on the movements of the snails.

Bovbjerg's experiments testing the reactions of the snails to a barrier to upstream movement repeat the findings of strong positive rheotaxis. They also demonstrate that aggregations may be formed as a result of such barriers. It's interesting to note that in each experiment two snails managed to pass the barrier and continue upstream movement. More may have done so in a similar experiment of longer duration. Details of the prevailing conditions are lacking, including current velocity and substrate type information.

A controversy, acknowledged by Bovbjerg, is set up by a comparison of his results with those of Allison. Allison, it will be remembered, found that Campeloma moves at random with respect to the direction of water flow. Bovbjerg found that Campeloma exhibit movement oriented against the current and move randomly only in the absence of a current. It is an objective of the present study to make a contribution toward the

resolution of this controversy and, in so doing, provide a more complete understanding of the behavior of these snails as exhibited by their movements and distribution.

## DISCUSSION AND CONCLUSIONS

One of the firmest conclusions to be drawn from the present study is that burrowing is the prevalent, nearly universal response to a penetrable substrate. This is the case regardless of which current velocity and light condition combination is being applied. Sand is the only substrate type used which Campeloma is capable of penetrating; floor is obviously impenetrable and the particle size range selected for gravel is too coarse for burrowing by the snails, although they are capable of moving into pockets of relative shelter. Examination of the results for movement on sand reveals that the means for the total extent of movement (terminal distance) range from 0.3 cm to 0.7 cm, including all combinations of current and light conditions. The maximum mean, 0.7 cm, is less than one third the lower limit for shell height of the specimens tested. Clearly, this is extremely slight movement for this animal. At the start of tests conducted in the light, six or seven or usually all eight of the snails were observed to begin burrowing into the sand at or within a centimeter of their starting positions. The snails appeared to burrow a little more rapidly in moving water than still, but other than this, current velocity had no apparent effect on their movement



on sand. The close similarity between final positions in the light and in the dark indicates that light condition had no apparent effect either. Of course, movement and burrowing in the dark were not directly observed but at the end of a test run, regardless of the light condition used, the snails were typically found partially or completely burrowed beneath the surface of the sand in an area within one centimeter, horizontally, of their respective starting positions. There was no observed tendency to return to the surface of the sand after a period of being buried or to move any appreciable distance (such as two or three centimeters) through the sand. Although this lack of movement is disappointing in that it fails to allow any comparisons among the effects of current velocities or light conditions, it provides support for the conclusion that Campeloma is indeed a burrowing snail and that when moving onto a penetrable substrate it will typically burrow. This is an important conclusion with valuable implications for the movements and distribution of Campeloma under natural stream conditions.

Campeloma has been described as a burrowing snail (Allison, 1942; Baker, F. C., 1911; Baker, H. B., 1922; Clench, 1962; Harman, 1972; Harman and Berg, 1971; van der Schalie, 1965) and is usually found buried in a penetrable substrate (Table 3). The evidence indicates

that silt-sand-mud substrates are the preferred habitats of this snail. Individuals can be expected to be found primarily or exclusively in such habitats within streams. Once situated in such habitats, the snails might be expected to exhibit little movement as long as chemical and physical conditions remain within tolerable ranges and the effects of predation or parasitism are not great. The food supply should usually be adequate. Campeloma showed little movement over sand in the 30-minute test runs and in pilot tests lasting up to six hours. The Campeloma tested by Shelford (1914) moved extensively over the exposed floor of the artificial stream device but, when placed on a sand substrate, soon burrowed and remained stationary. From both laboratory and field observations, Cummins and Lauff (1969) conclude that many species of stream benthos exhibit habitat selection primarily on the basis of substrate particle size and/or food supply. Harman (1972) reaches much the same conclusion pertaining specifically to freshwater mollusks. These conclusions imply that once an animal has reached and selected a microhabitat through movement, it will be likely to remain within that microhabitat at least as long as environmental conditions are stable and there is no internal change leading to further migration. This seems to be characteristic behavior for Campeloma. Even with the extreme changes in current velocity and light

condition applied in the present study, the snails exhibited the same behavior of burrowing and remaining in place. F. C. Baker (1918b) describes the Campeloma of Oneida Lake, New York as being "confined to restricted areas" of sand or clay substrates. Allison (1942) found that his bait traps were ineffective in lakes and suggested that this might be due to the presence of sufficient food to "nullify the effects of food concentrated at traps", indicating that Campeloma in a food-rich microhabitat show little movement. Bovbjerg (1952) observed increased densities of the snail in marginal areas of the stream, areas characterized by fine substrates, low current velocity, and concentration of detritus. I have observed the same situation on numerous occasions. These observations indicate that such microhabitats tend to retain individuals which have reached them. Bovbjerg (1952) also observed aggregations of Campeloma downstream from apparent barriers to upstream movement. This is a situation which has also been frequently observed by myself and other investigators. The snails are typically found buried in a fine substrate which has accumulated in the lee of the obstruction. The question arises as to whether the aggregation (and hence a lack of movement) is due primarily to the insurmountability of the barrier itself or to the favorability of the microhabitat created by the barrier. Schmid

(personal communication) favors the latter viewpoint. Bovbjerg (1952) himself offers the self-contradictory explanation that "the clue appears to be in the burrowing habit. In the stream and chute the animals accumulated in the gravel substratum below the block, unable to utilize the surface detour. It is probable that this feature of the animals' behavior accounts for its relative inability to negotiate rapids." The question remains as to whether the snails fail to pass a barrier because they are physically unable to do so or because they don't even attempt to do so (behaviorally unlikely to do so).

In addition to and accompanying these indications of a lack of movement there are indications of frequent and extensive movement both within a suitable microhabitat and between suitable microhabitats. Given sufficient time, the Campeloma which I tested on sand, as well as those tested on sand by Shelford (1914), may have shown considerably more extensive movement. Snails maintained in the holding tanks and those kept in aquaria with substrate collected from a stream bed both exhibited more movement than was shown in tests on sand in the flume. In the field, I have observed individuals in the act of moving within what appeared to be a uniform microhabitat. In a matter of days and sometimes hours there are often noticeable changes in densities from place to place

within a suitable microhabitat. The very fact that bait traps work is an indication of frequent movement within a microhabitat and an indication that variation in food concentrations may be an influential factor. My own observations on this matter are corroborated by those of Allison (1942) and Shoemaker (1961). Bovbjerg (1952) observed steady and extensive upstream movement over substrates which the snails apparently could penetrate, although it's not clear just how penetrable or how suitable as microhabitats those substrates were. Medcof (1940) observed frequent movement within what was apparently a suitable microhabitat in a mill pond. The Campeloma were concentrated in a band around the pond which represented a depth range of less than one inch to about one foot. The snails remained within this depth range in spite of frequent rapid fluctuations in water level brought about by operation of the mill. "In some cases they were observed to travel as much as 12 ft. overnight in places where the beach sloped gently."

There is ample evidence that Campeloma travels between, as well as within, favorable microhabitats. Active dispersal by upstream movement is by far the most feasible explanation of observed distributions of Campeloma in streams and watersheds. "Migration through the water is a major means of natural dispersal for all fresh-water mollusks and it is the only important means

for the gill-breathing prosobranch snails" (Harman and Berg, 1970). In small streams such as Mill Creek, colonies of Campeloma are located in favorable microhabitats isolated by stream sections which often include hostile (to Campeloma) riffle environments. The snails are found in locations many kilometers and numerous riffle sections and barriers upstream from their presumed original source, in this case the Grand River. To establish such a distribution, individuals must leave suitable or favorable microhabitats and travel through areas where environmental conditions are markedly less favorable before again reaching areas of low current velocity and fine, detritus-rich substrates which favor their growth and reproduction. This must occur repeatedly or continuously through time and against the setbacks afforded by drift, which may be considerable during spates. Colonies of Campeloma may be reduced or absent from a site from one year to the next and this may often be attributed to removal by spates (Anderson, 1966; van der Schalie, 1965). Field observations provide strong support for the inference that Campeloma in streams move long distances and between the more favorable microhabitats. Goodrich (1932) notes that in the Huron River, Campeloma can be found among plants in fast water along the banks in the spring but "later in the year, such situations are apparently abandoned for

muddier localities". H. B. Baker. (1922) found C. decisum buried in pockets of sand scattered about on a rocky river bed. The distribution of C. decisum in the section of Dickerson Creek studied by Bovbjerg (1952) is suggestive of considerable upstream movement, including passage through sub-optimal microhabitats. The snails appear to have surmounted two rapids-barriers within the section studied and a few were directly observed to surmount rapids created in a chute. Indeed, field observations also provide direct evidence that lotic Campeloma travel long distances and pass through marginally favorable and unfavorable microhabitats. The closest and most detailed of such observations are those of Bovbjerg (1952). He noted extensive upstream movement by nearly all the individuals examined at lower and higher current velocities and in and out of experimental chutes. On the basis of his observations, Bovbjerg (1952) reaches the conclusion that observed distributions of Campeloma in streams can be adequately explained by migration through the water. He states that "barring setbacks by spring flood waters, which undoubtedly occur, C. decisum is able to rapidly populate a stream. This could occur after chance introduction into an established stream, or by slowly pushing up tributaries with the developing drainage patterns over a long period of physiographic history. It should be noted that the few

individuals able to pass a barrier would have little difficulty repopulating the upstream stretch of the stream." F. C. Baker. (1928b) directly observed long distance movement by Campeloma. When a number of creeks were transformed into lakes by the building of a dam, many of the Campeloma traveled two to three miles or more upstream into unchanged stream sections. Van Cleave (1934) noted that local exterminations of Viviparus by pollution in the Illinois River were followed by repopulation from any remaining individuals or upstream movement from colonies in cleaner water. The same process was undoubtedly taking place for the closely related Campeloma, which were also present.

So it can be seen that, although burrowing is the prevalent, nearly universal response to a penetrable substrate, as indicated by my experimental evidence and that of Shelford (1914) as well as by the field observations of numerous investigators and myself, movement does take place both within and between areas of penetrable substrate. Whenever Campeloma exhibits such movement, it does so under the combined influences of environmental factors, the most important of which are substrate type, current velocity, and food supply. Furthermore, the present study reveals that the presence or absence of light has an important influence on movement and one which has been generally ignored in the case of



Campeloma. It is the primary objective of this study to evaluate the influences of substrate type, current velocity, and light on the movement and distribution of C. decisum. Although it may be concluded that the snails typically burrow upon encountering a penetrable substrate, it may also be concluded that they eventually move again. Both conclusions, with all their ramifications, must be taken into account to obtain a comprehensive understanding of the distribution of C. decisum at any point in space and time.

The second major conclusion which I have reached is that the rate of movement over an impenetrable substrate is related to the type of surface it presents. Movement is steadier and more rapid over a smooth surface than over a more rugged one. This conclusion has logical appeal on the basis that a path of given vertical relief should require more time and energy to traverse than any path of lesser vertical relief. An additional, possibly more important factor may be operating in the case of Campeloma. The pockets of relative shelter from current and light afforded by sufficiently coarse substrates may act as substitutes for the shelter obtained by burrowing in a penetrable substrate.

I am aware of only one comparable study involving gastropods which bears on this conclusion. Moore (1964) found that Stagnicola palustris and Physa propinqua

tested in an artificial stream differed in their ability to remain attached to various substrates. Dislodgement by current occurred, in decreasing magnitude, on sand, clay, caliche rock, plexiglass (the flume floor), pea gravel, and basalt rock. Thus the ability to remain attached depended upon the stability and slipperiness of the surface as well as its smoothness.

The two impenetrable substrates used in the present study were floor and gravel. Floor presented an extremely smooth and uniform surface whereas gravel, although it was leveled out in the flume, provided vertical relief greater than the maximum shell height of the tested snails. This sharp contrast in surface conditions was mirrored in the movements of the snails. Although under all conditions equal to or greater than movement on sand, movement on gravel was nonetheless negligible. Mean terminal distances for movement on gravel ranged from 0.7 cm to 2.4 cm. This compares to mean terminal distances ranging from 19.0 cm to 41.4 cm on floor.

The discrepancy between movement on gravel and floor seems too great to be explained solely by the difference in ease of travel over the two dissimilar surfaces. In spite of the ruggedness of the gravel surface, a snail is unquestionably capable of traveling more than one or two centimeters over it in 30 minutes time. And, indeed, during test runs on gravel in the light, the snails

rarely exhibited continuous movement for the full test period. They tended rather to move from their starting positions only so far as the first or second surface depression about the size of a shell encountered. Once in such a depression, an individual typically remained there for the duration of the test.

I believe that the best explanation for this behavior is that the snails, seeking shelter but being unable to burrow, are utilizing whatever shelter they encounter. The behavior is one of shelter-seeking and the depressions in the gravel surface are a substitute for the shelter provided by burrowing. This may also account for the extensive movement over floor; no shelter is available and movement, therefore, is continuous. According to Carthy (1958), in the search for suitable microhabitat situations, any place which provides the sought after conditions will be satisfactory. Shading, protection from the direct force of the current, and concentrations of food would all be optimal in the pockets of gravel in the absence of the even more suitable microhabitat of a penetrable substrate.

The burrowing habit of Campeloma may make it unique among lotic gastropods in respect to movement for feeding purposes. Scott (1966) found that the prosobranch gastropod Potamopyrgus badia preferred smooth, exposed surfaces on the stream bottom. "It is suggested that

travel over coarse sand and fine gravel would result in irregular contact of the radula with the film of algae and detritus. On the other hand travel across a large smooth surface would permit continuous feeding."

Campeloma appears to be able to feed while stationary. Being buried in a detritus-rich substrate or positioned in a gravel surface pocket where detritus is likely to accumulate seem much more advantageous to Campeloma than continuous movement.

My third major conclusion is that movement in standing or slowly flowing water is either at random or directed toward food concentrations with gravity, ambient light intensity, and any current velocity having little or no influence. On the basis of the present study, I will define slowly flowing water as moving at a velocity of 8 cm/sec or less within 3 cm of the substrate surface. Such current conditions were maintained in the still water test runs and are to be found in pools and other sheltered areas of streams.

Relevant evidence from the present study is drawn exclusively from the results for movement over floor. This is because movements over sand and gravel were too slight to be applied meaningfully toward this conclusion. The much more extensive movement over floor permits meaningful comparisons among results for the various current velocity and light conditions. As an individual

snail moves over the floor, it does so at a rate and in a direction influenced by the ambient conditions of current velocity and light. Likewise, an individual moving over the substrate of a natural stream, whatever type of substrate it may be, will also move in a direction and at a rate influenced by such environmental factors as current velocity, light intensity, and food supply. Thus, although floor is probably the experimental substrate type least similar to natural types, it is the one from which the most useful information concerning movement can be obtained. As the discussion of my previous two major conclusions indicates, the relative lack of movement exhibited on sand or gravel is, in itself, of great value in understanding several aspects of the behavior of the snails. However, more extensive movement is required for an analysis of the influence of all the important environmental factors.

The results from tests in still water and on floor are the most useful for this discussion. Mean terminal location in both light and dark was within 2.5 cm of the starting line (Table 18). Mean terminal distance was 24.4 cm in the light and 19.0 cm in the dark. These facts indicate that although movement was extensive in both light and dark it was not predominantly upstream or downstream in either light or dark. The snails moved essentially at random, without any indication of

influence by light condition or gravity. The means for percentages of individuals moving upstream, downstream, or not moving lend some further support to this conclusion. In the light, nearly the same percentage moved upstream as downstream with none failing to move. In the dark, however, 6.3% of the snails failed to move and about two-thirds moved downstream. These last results are the only ones inconsistent with the conclusion that light and gravity have little or no influence on the direction of movement in still water. Of course, food supply was not a variable used in the test runs.

In laboratory studies conducted in still water, Shelford (1914) also observed Campeloma moving in a random fashion. Individuals of the species Campeloma subsolidum, when tested for reactions to substrate type, wandered around in the test area until they burrowed in a sand substrate. C. subsolidum tested for reaction to a light intensity gradient, also in still water, remained inactive. In his current reaction tests, Shelford (1914) recorded orientation and not movement but his results, described earlier, still merit a review here. In a current velocity range of 4 to 6 cm/sec, which I have defined as slowly moving water, 50% of the individuals showed a positive orientation and the other 50% showed a negative or indifferent reaction or no activity. With an increase in velocity to 10 to 12 cm/sec, 80% of the

individuals oriented positively and 20% showed no activity. So, in terms of orientation only, Shelford (1914) found that Campeloma are influenced considerably less by slowly moving water than by a more rapid flow.

As mentioned earlier, Allison (1942) and Bovbjerg (1952) disagree concerning the rheotactic responses of Campeloma. Allison (1942) observed the snails moving upstream, downstream, and across the stream and concluded that they move at random. Unfortunately, he provided no direct indication of the current velocity although it does not appear to have been very great. Bovbjerg (1952), however, reports a high degree of positive rheotaxis for Campeloma decisum tested in a flume placed in a natural stream. At 25 cm/sec, a mean of about 85% of the 600 snails tested moved upstream. At 5 cm/sec, within my "slowly flowing water" range, a mean of nearly 88% moved upstream. The latter result is in disagreement with my conclusion. However, Bovbjerg (1952) also tested the snails for geotactic response in still water and found that nearly the same number of snails moved toward each end of both level and sloping flumes. He states that "the tendency was apparently to move randomly near the release point". This corroborates my results for still water tests and indicates that gravity has little or no influence on the direction of movement.

My results and those just reviewed provide considerable support for the conclusion that movement in standing or slowly flowing water is influenced little or not at all by gravity, ambient light intensity, and any slight current and that movement under such conditions is at random. The possibility of directed movement under the influence of food supply remains for consideration. Movement in standing or slowly flowing water may not be at random but rather in a direction determined by response to concentrations of food. This possibility was not tested for in my experiments but it must be considered to achieve a reasonably full understanding of the movements and distribution of Campeloma in streams.

There are two types of animal movements according to the system of classification developed by Fraenkel and Gunn (1961). These are kineses and taxes. "Kineses are defined as the effects exerted by stimuli on the rate of random movements" (Savory, 1959). If the effect is exerted simply on the rate of movement, it is orthokinesis. If the effect is exerted on the rate of change of direction of movement, it is klinokinesis. "Taxes, on the other hand, are orientated movements resulting from responses to the direction from which the stimulus arrives" (Savory, 1959). I hypothesize that, in standing or slowly flowing water, the movements of Campeloma in natural streams may be characterized as klinokinesis.



Movement is at random and the rate of change of direction is influenced by olfactory stimuli derived from concentrations of food. According to Wells (1968), scavenging gastropods exhibit klinokinesis in still water. In more rapidly flowing water, I hypothesize that the movements of Campeloma are taxes. Movement is oriented according to directional stimuli provided by the current, which is rheotaxis. If the current carries diffusions from food concentrations, the movement is also chemotaxis. The strength of the current bearing the chemical stimuli determines whether movement is klinokinesis or chemotaxis.

There is a good basis for assuming that Campeloma has the sensory capacities prerequisite to such behavior. Prosobranchs possess osphradia (Charles, 1964). The osphradium is an organ which has been shown to be a chemoreceptor. Located in the mantle cavity of prosobranchs, in the path of incoming water, the osphradium is apparently capable of detecting food solutes in the ambient water. "The function of the osphradium as a distance chemoreceptor has been demonstrated by behavioral experiments in three species of prosobranch and one basommatophoran" (Charles, 1964). The osphradium of Campeloma can be expected to have such capabilities, particularly since distance chemoreception is especially important in the feeding behavior of scavenger gastropods (Owen, 1964).

For Campeloma, klinokinesis in response to food stimuli may take place as follows: A hungry snail moves about, essentially at random, until it senses the presence of a food source such as a dead animal, dung, or a concentration of detritus. As long as the stimulus increases in strength, the snail maintains a direct course. Whenever the stimulus weakens, the snail changes direction until it increases once again. In this manner the snail eventually comes upon the source of the stimulus; the food. Chemotaxis is more direct. The current bears the stimulus downstream and the snail moves upstream, with relatively little deviation, to the food. It is apparent that klinokinesis can occur only in still or slowly flowing water. In more rapidly flowing water, the snail has no conceivable means of detecting food sources which are downstream or even across the stream from its position.

Neither klinokinesis nor chemotaxis in response to food stimuli have been studied in the case of Campeloma. However, there is at least one report involving other species which seems particularly relevant. Copeland (1918) investigated the olfactory reactions of the marine whelks Alectrion obsoleta and Busycon canaliculatum. Both species are prosobranchs, both are scavengers, and both burrow in the substrate. Both

species possess a siphon, an extended fold of the mantle through which water is drawn into the mantle cavity.

Campeloma lacks the siphon but this difference should only make Campeloma less efficient in chemoreception than the whelks. There is no essential difference in the mechanisms involved. Drawing from his extensive investigations, Copeland (1918) proposed the following scenario:

Let us assume that a whelk is crawling over the sea bottom in the vicinity of a dead fish. From what has been learned of its olfactory reactions under varied conditions, it is possible now to picture mentally the movements which must often occur after the snail scents the food, and to interpret them with some degree of success. As the snail moves, the end of the siphon is shifted from one side to the other, although the foot is carrying the animal in a straight course. Perhaps as the siphon is directed laterally, it happens to enter a stream of odorous material spreading or drifting from the fish, a sample of which passes to the osphradium and stimulates it. The effect is seen in the foot which begins to turn in the direction of the odor. The siphon, next directed away, fails to receive the stimulating substance, but on the return swing again enters it, the osphradium is again stimulated and the animal moves into the stream of odorous material, swinging its siphon vigorously. The snail continues turning as long as the osphradium is most strongly stimulated by materials coming to it from one side of the siphon's axial position. It may be said to be oriented to the odor stream when the foot is straightened out, and the effective stimulating substance is received by the siphon in its axial position, or when it is equalized on both sides of that position. The siphon continues conducting to the osphradium samples of water and odorous substance in changing concentrations from the region through which it moves; stimulations of the osphradium are followed by foot movements which take the snail toward the place where the strongest

stimulating material entered the siphon, until slowly but surely the animal is directed to the source of the scent.

Campeloma, lacking the siphon, would have to make bodily turns more often than the whelks but, except for this, it might well exhibit similar behavior under similar circumstances.

In the preceding section I have attempted to show that movement by Campeloma in standing or slowly flowing water is either at random or is directed toward concentrations of food. Under these conditions, gravity, ambient light intensity, and any slight water flow appear to have little or no influence on movement. However, in moving water of moderate or greater velocity, the rate of movement is greater and the direction of movement is more strongly influenced by the ambient current velocity and light condition. This forms my fourth major conclusion.

By moderate or greater velocity I mean a current velocity greater than 8 cm/sec within 3 cm of the substrate surface. In the artificial stream device, moderate velocity was 8 cm/sec and fast velocity was 14 cm/sec. In natural streams, current velocities of 8 to 14 cm/sec and higher may be found at myriad points, including parts of pool sections as well as riffles and intermediate sections.

A comparison of movements over floor in still water, moderate velocity, and fast velocity (Table 18) provides

information relevant to this conclusion. The rate of movement of the snails, as indicated by the mean terminal distances, is significantly greater in the light in both moderate and fast velocities than in the light in still water. It is also significantly greater in the dark in both moderate and fast velocities than in the dark in still water. Thus moving water appears to stimulate the snails to more extensive movement than that which they exhibit in still water. Not only is movement more rapid and extensive in flowing water, it is also more strongly directional. Both current velocity and light condition exert influences of significant magnitude on the direction of movement. At moderate velocity, in the light, the mean terminal location is 18.4 cm upstream whereas in the dark it is 6.6 cm downstream. At fast velocity the relationship is reversed. The mean terminal location in the light is only 3.2 cm upstream and in the dark it's 14.8 cm upstream. Whatever the reasons for these contrasting behaviors, it is clear that current velocity and light condition are interacting factors and that both influence the direction and extent of movement by the snails. This is an especially important finding because no other study has investigated the influence of light condition on movement. As discussed earlier, mean terminal locations in still water were within 2.5 cm of the starting line in both light and dark. Mean terminal

locations in moderate and fast velocities range from 1.3 to 7.4 times as great. The snails tended to travel further upstream or downstream in moving water than in still. Also, significantly greater percentages of individuals moved upstream in the light in moderate and fast velocities than in the light in still water and the same relationships hold in the dark. About two-thirds of the individuals moved upstream in the light at moderate velocity and in light and in dark at fast velocity. Thus, in moving water, movement is more directional and, specifically, upstream than in still water. My results indicate that moving water of moderate or fast velocity increases the rate or extent of movement of the snails over that exhibited in still water. Movement is more strongly directional, primarily in the upstream direction, in moving water than in still and the influence of the ambient light condition on movement is greater in moving water than in still.

When I refer to moderate or greater velocity in the discussion of this conclusion it should be understood that there is an upper limit to the range of velocities over which the conclusion applies. There is a velocity at which an individual snail can no longer maintain its hold on the substrate and is washed away. That velocity may depend upon the type of substrate and size of the snail, as Moore (1964) found to be the case in laboratory

studies on Stagnicola palustris and Physa propinqua. The upper limit need not be great because the force exerted by flowing water varies as the square of the velocity (Coker, 1954). In the case of the Campeloma tested, the upper limit is definitely greater than 14 cm/sec. Below the maximum which can be withstood, there is a range of velocities over which the snail can maintain its hold but seems capable of little or no movement. This conclusion applies to the range of velocities from moderate to those at which the snails are capable of movement without being washed away. As discussed in the preceding section, the Campeloma tested by Shelford (1914) for orientation to current were more strongly influenced by a 10 to 12 cm/sec current velocity range than by a 4 to 6 cm/sec current velocity range. However, a further increase in velocity to a 16 to 20 cm/sec range resulted in 90% of all individuals tested showing no activity. This may be at least a part of that range of velocities over which the snails merely maintain their positions and exhibit little or no movement. In the case of the two lower velocity ranges, Shelford's (1914) findings, although concerned only with orientation, tend to corroborate my findings that in moderate or greater velocities, up to the limits just described, movement is more strongly directional than in lower velocities or still water.

Bovbjerg's (1952) semi-natural stream tests involving 600 Campeloma decisum resulted in about 85% to 88% of the snails moving upstream at both the less than moderate current velocity of 5 cm/sec and the high velocity of 25 cm/sec. Thus these sharply dissimilar velocities had closely similar influences on movement. However, in still water tests Bovbjerg (1952) found that the snails moved essentially at random. So an increase in velocity from 0 to 5 cm/sec was sufficient to give a strongly directional influence to the movement of the snails and the direction was primarily upstream. Allison (1942) also observed random movement by Campeloma. But he didn't report current velocity and without that information his results have only a speculative relevance to the conclusion presently under discussion.

If the rate and direction of movement of Campeloma are influenced by current velocity, then this response which they show is one of rheotaxis. The snails move differently in flowing water than in still water, indicating a rheotactic response. The snails move differently in moderate or greater velocities of water flow than in less than moderate velocities, indicating that their rheotactic response is sensitive to current strength and not merely on or off. Furthermore, I have found that the presence or absence of light has an influence which varies with the strength of the current. It is



important, then, to examine the phenomenon of rheotaxis as it pertains to Campeloma.

The meanings of kinesis and taxis were described earlier. Rheotaxis is a taxis in response to flow of the ambient medium (Fraenkel and Gunn, 1961). In the preceding section I hypothesized that, in moving water of moderate or greater velocity, movement by Campeloma is orientated according to the directional stimuli provided by the current. In this section I have provided evidence in support of this hypothesis. Movement in flowing water of less velocity or in still water may be described as random movement or as klinokinesis.

Olfaction may at times play a role in the rheotactic reactions of Campeloma. If a current is relatively strong and bears chemical stimuli, the reaction may be chemotactic. If a current bearing chemical stimuli is relatively weak, the reaction may be one of klinokinesis. The reactions of rheotaxis and chemotaxis may at times be inseparable. If a current carries food solutes to a snail, the positive rheotaxis exhibited by the snail in that current may be reinforced or even replaced by positive chemotaxis. It is difficult in such a situation to determine which is predominant. Some animals respond to current only if it bears chemical stimuli (Carthy, 1958). My results indicate that Campeloma can exhibit rheotaxis independently of chemotaxis.

Other forms of sensory perception are undoubtedly operative in the rheotactic responses of Campeloma. It is possible that the snails are able to sense current velocity by visual perception of suspended particles moving with the water. Although vision in Campeloma has not been studied, they are certainly able to detect at least large changes in light intensity and it seems likely that they can detect movement (Charles, 1964; Kaestner, 1967). It may not be true of Campeloma but the eyes of some prosobranchs are thought to be "structurally adequate to form sharp images" (Charles, 1964). The interaction between light condition and current velocity shown in my results indicates that vision does indeed play a role in the perception of and reaction to current velocity by Campeloma. While it is clear from my results that the snails do not require light to perceive water movement, it is also clear that the presence or absence of light has a strong and important influence on their response to water movement. This was formerly not known.

Touch is another sense which may be involved in the perception of current velocity by Campeloma. The tentacles of gastropods "contain a well developed tactile sense" (Charles, 1964). The tentacles could be the site of concentrated tactile receptors responsible for the detection of currents but this remains conjectural. The head region of planarians and the antennules of

crustaceans appear to be provided with current receptors (Carthy, 1958). Aquatic insects commonly use a combination of visual and tactile stimuli for maintenance of position in a stream. Fraenkel and Gunn (1961) state that for planarians and probably gastropods as well, "it is not the receptors in contact with the ground but special current-receptors which are responsible for the rheotactic reaction". My results show that in the dark and with olfactory stimuli controlled, the snails behave differently in still water, in moderate velocity, and in fast velocity. This indicates that tactile receptors do function in the detection of the presence, strength, and direction of water flow. As shown in Table 18, movement in moderate velocity is strongly upstream in the light but slightly downstream in the dark. At fast velocity, however, a mean of about two-thirds of the snails move upstream in both light and dark and the mean terminal locations are both upstream and not significantly different. These results are indicative of what may be a reversible hierarchy of importance involving the visual and tactile senses. In the relatively weak moderate velocity, visual stimuli made possible by the light appear to be the predominant stimuli for the rheotactic reaction. Under the strong influence of fast velocity, however, the rheotactic reaction is pronounced in both light and dark. Thus tactile stimuli seem to be predominant at fast velocity.

The following is a hypothetical description of the movement of Campeloma under natural conditions in moderate and greater velocities (up to the velocity limit previously described): Random movement and klinokinesis exhibited at lower velocities are replaced by taxes; simple rheotaxis in the absence of olfactory stimuli from food sources and some combination of rheotaxis and chemotaxis in the presence of such olfactory stimuli. If the current velocity is in the neighborhood of moderate (8 cm/sec), the snails will typically move upstream in the daytime and virtually at random or somewhat downstream at night. If the current velocity is in the neighborhood of fast (14 cm/sec) and higher, the snails will typically move upstream in the day or night. By "typically move upstream" I mean that about two-thirds or more of the individuals involved will exhibit positive rheotaxis. In addition, the snails will tend to move at a faster rate than in still water or less than moderate current velocities.

In discussion of the latter two preceding conclusions, but especially the last, one conclusion I have sought to establish is that Campeloma exhibits positive rheotaxis not absolutely but rather to an extent dependent upon the ambient conditions of current velocity and light in combination. This forms the conclusion

presently under discussion. Not all Campeloma living in streams exhibit positive rheotaxis at all times although the stream is constantly flowing. The strength of the current and the intensity of the light (at least the extremes of daylight and the darkness of night) influence the occurrence of rheotaxis, the sign of rheotaxis, and the rate of movement. Furthermore, these two environmental factors interact in their influence; one should not be considered without the other. Therefore, although the generalization can be made that Campeloma exhibits positive rheotaxis, there are both exceptions and complications of considerable importance.

The occurrence of positive rheotaxis is widespread among members of the stream benthos. There is "a substantial body of evidence that invertebrates can and do move upstream by active migration against the direction of flow, and this behavior is, of course, an important adaptation enabling them to live in running water" (Hynes, 1970). As I have mentioned earlier, active upstream migration is by far the most likely means of dispersal for Campeloma. However valid positive rheotaxis may be as a generalization, its expression in particular instances is far from consistent. Of the nine insect species and one pulmonate species (Helisoma anceps) tested in an artificial stream by Cummins and Lauff (1969), three of the insect species tended to move

downstream, two upstream, and four attached, burrowed, or showed no particular orientation. Helisoma showed both positive rheotaxis and a lack of rheotaxis, depending on substrate conditions. Of course, this is not to say that the negative and indifferent species never exhibit rheotaxis in general or positive rheotaxis in particular. Rheotaxis, like most if not all forms of behavior, is neither simple nor universal.

The two major studies on the movements of Campeloma in streams have presented rheotaxis as a rather simple and absolute form of behavior. Allison (1942) concluded that the snails do not exhibit rheotaxis but move at random. Bovbjerg (1952) found that more than 85% of the snails he studied exhibited positive rheotaxis. I have mentioned these opposing conclusions several times before. I believe that my laboratory stream investigations have contributed toward a solution to this controversy. The main source of disagreement is the superficiality of the conclusions regarding rheotaxis. Both apparently contradictory conclusions can be reconciled as parts of a more comprehensive description of rheotaxis in Campeloma. Under conditions of low current velocity, the snails may indeed move at random or exhibit klinokinesis in the presence of a concentrated food source. Under conditions of higher current velocity, most of the snails will typically exhibit positive rheotaxis, possibly

reinforced by a chemotactic response to food. These movements seem to be characteristic in conditions of light. In the dark, however, positive rheotaxis is less pronounced at moderate velocities (from around 8 cm/sec to around 14 cm/sec) but remains minor at low velocities and dominant at high. Light condition, then, influences the rheotactic response and not simply so but through interaction with current velocity. I have already presented arguments for these points and I will not repeat them here. I want to stress my conclusion that the rheotactic response of Campeloma is not merely on or off, as the conclusions of Allison (1942) and Bovbjerg (1952) suggest. Their findings are not false. They are too limited in scope to adequately describe the behavior. The rheotactic response of the snails is, in fact, variable and its expression is dependent upon the influences of the ambient conditions of current velocity and light in combination.

Summary - the Movements and Distributions of Campeloma  
decisum in Small Streams

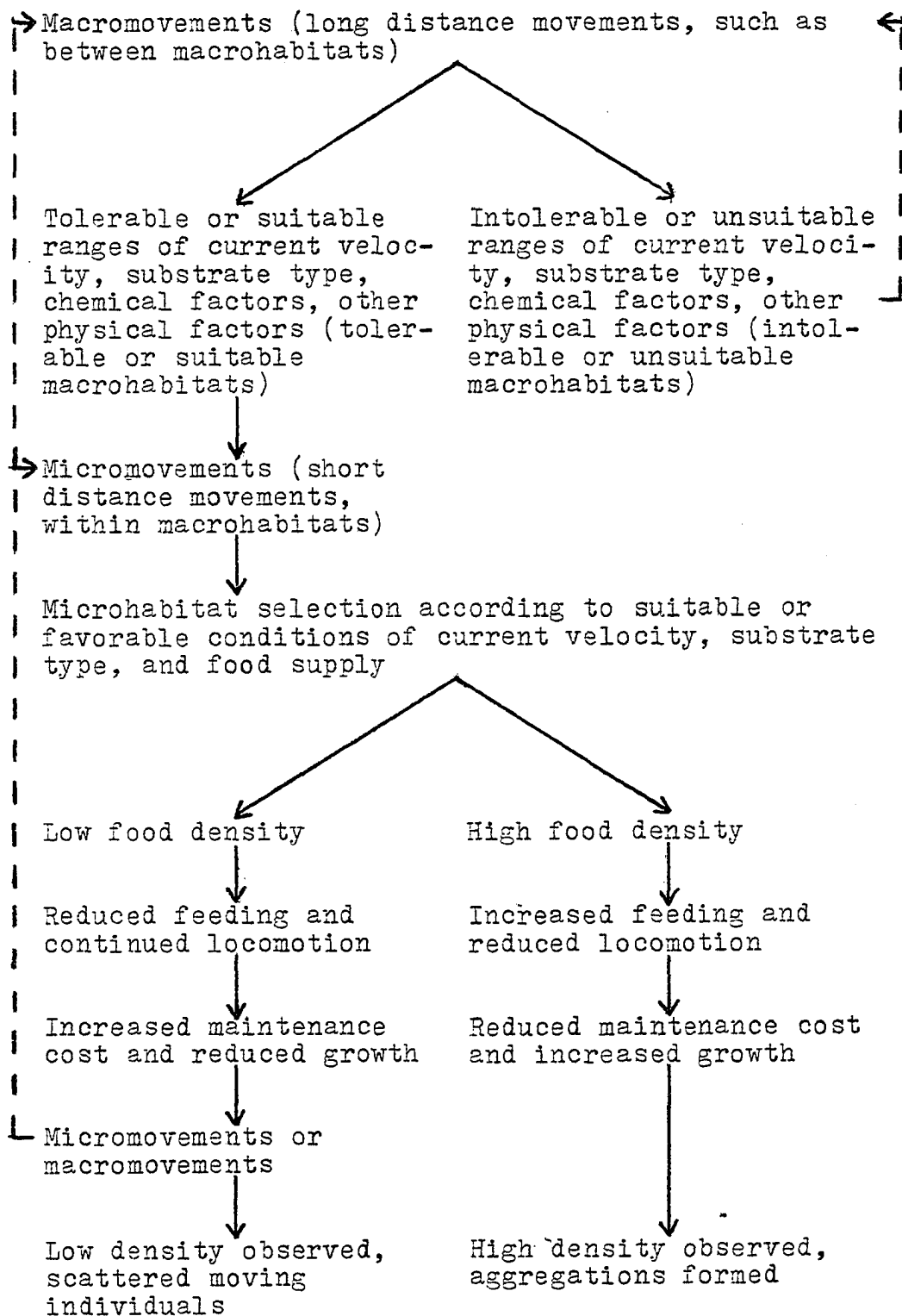
In discussion of the preceding five conclusions, I have integrated interpretations of my results with pertinent information from the literature. It has been my intention in so doing to present a more comprehensive analysis of the movements and distributions of Campeloma

decisum than could possibly be achieved on the basis of my experimental results alone. If fact, my results, taken alone, can be used with strict validity only in application to the artificial stream situation from which they were derived. However, my results can be used, with appropriate caution, to make inferences about the behavior of the snails in natural stream settings. When these inferences are made in the light of pertinent information from the literature, including the complimentary natural stream investigations of Allison (1942) and Bovbjerg (1952), they provide a reasonably accurate and inclusive account of the movements and distributions of Campeloma decisum in small streams. Of course, there remains much about this account which is hypothetical and, hence, there remains a need for further research.

The purpose of this section is to summarize the account of the movements and distributions of the snails. It is, therefore, a summary of my discussion. To maximize conciseness, I am presenting this summary in the form of a diagram, which is shown in Figure 1. This diagram is adapted from Figure 2 of Cummins (1972). The adaptations of the snails to their habitats, as depicted in Figure 1, will be "considered primarily energetic, with problems of concealment from predators and competition secondary" (Cummins, 1972). The primary problem of survival for Campeloma is obtaining sufficient food for



Figure 1. The kinds of movements exhibited by Campeloma, the conditions inducing them, their relationship with feeding and growth, and the resultant distributions.



respiration, growth, and reproduction. From what is known of the ecology of Campeloma, neither predation nor competition appear to be of any more than marginal importance for most populations. In use of the energy obtained from food, "the most costly portion is respiration, with growth (and reproduction) being accomplished only after that cost is assigned. Since highest respiration costs are closely linked to locomotion, that activity can be viewed as being in direct 'competition' with growth" (Cummins, 1972). The more energy required for movement to obtain sufficient food, the less energy is available for the processes of growth and reproduction. Therefore, "the general strategy" of the snails "is to minimize locomotion and maximize feeding, thereby maximizing growth" (Cummins, 1972). This is the basic reasoning in the design of Figure 1, which relates locomotion with feeding and growth.

In following the flow of Figure 1, the most appropriate place to begin is with macromovements. Macromovements are movements covering relatively large distances. Movements from one macrohabitat (pool or depositional, riffle or erosional, intermediate) to another are macromovements, whether these macrohabitats are adjacent or separated by others. Obviously, longer movements are also macromovements. In some cases, movements within macrohabitats may be considered macromovements if they

are sufficiently great, as from one end to another of a large macrohabitat.

Macromovements are initiated and maintained by the existence of ambient conditions which are intolerable or unsuitable to the snails. Intolerable conditions may result in death if they are not escaped or changed. Unsuitable conditions may inhibit or stop growth or reproduction although they can be survived. The intolerable or unsuitable conditions may be those of current velocity, substrate type, chemical factors, or other physical factors. I have already discussed the known and probable importance of several of these factors for the stream benthos and Campeloma. Such conditions may be brought about by gradual changes or by sudden changes like flooding or a large increase in the rate of introduction of pollutants. A snail in drift may be suddenly introduced into a macrohabitat with such conditions. Macromovements may be guided predominantly by positive rheotaxis for Campeloma. If the current velocity is fast, the rheotactic response will be strongly positive. If the current velocity is moderate, positive rheotaxis will be weaker, especially in the dark. At these velocities and in slowly flowing or still water, positive or negative chemotaxis may also play a role in macromovements. In still or nearly still water, macromovements may be random movements continuing until the intolerable

or unsuitable conditions are escaped by traveling a sufficient distance.

Macromovements are terminated by arrival in a macrohabitat providing tolerable or suitable conditions. If conditions are tolerable but unsuitable, macromovement may be resumed failing the discovery of suitable conditions within the macrohabitat. If conditions are suitable as well as tolerable, macromovement can be considered more permanently terminated. The termination of macromovement blends into the initiation of micromovement. Micromovements are movements covering relatively small distances. Movements within macrohabitats, from one microhabitat to another, are micromovements. Micromovements are undertaken in the process of microhabitat selection by the snails. The environmental factors of primary importance in influencing microhabitat selection by Campeloma are current velocity, substrate type, and food supply. Once again, I want to stress that these factors are closely interrelated. Micromovements will be instances of positive rheotaxis if the current is sufficiently strong and may be reinforced by positive chemotaxis in response to concentrations of food. In lesser currents, micromovements may be by klinokinesis in response to food or at random. Micromovements in flowing water may vary in rate and direction with the presence or absence of light (day and night).

Microhabitat selection by Campeloma will be primarily on the basis of conditions of current velocity, substrate type, and food supply. Continuing from the viewpoint of energetics, food supply is the factor of particular importance among the interrelated three. A concentrated supply of organic detritus, with its associated bacterial and fungal populations, appears to be the key factor in making a microhabitat favorable to Campeloma. Of course, if the current velocity is too great the food will be unreachable or will itself be washed away. If the substrate particle size is fine, the food will probably be present in the form of deposits mixed with the inorganic particles and the snails can burrow and feed in the substrate itself. Micromovements will tend to be from one site of burrowing to another in the area of penetrable substrate. If the substrate is coarse and impenetrable, the food, when present, will be concentrated in depressions and cavities scattered among the stones. Micromovements will tend to be from one such depression or cavity to another nearby. Food in the former case is more uniformly distributed and easily reached than in the latter case. Substrate type and the distribution of food may be determined by current velocity. These relationships have been discussed previously in the present paper. So, although food supply is the key factor among the three, especially from the viewpoint

of energy needs, the importance of the other two factors and the interrelatedness of the whole cannot be ignored.

The presence of a high food density in a microhabitat, then, is the most favorable condition leading to the selection of that microhabitat. Once a snail reaches such a microhabitat, whether by klinokinesis or positive rheotaxis and chemotaxis, it tends to remain within it and feed. There is thus increased feeding and reduced locomotion. This leads to reduced maintenance cost and increased growth. Microhabitats with a high food density are favorable to growth and reproduction. Campeloma will often be found at high densities in such microhabitats and in macrohabitats, typically pools, containing many such microhabitats. Large aggregations may be formed around especially dense food concentrations.

A microhabitat including a low food density is less favorable to Campeloma. The lack of food means reduced feeding and this leads to continued locomotion. As a result, the snails experience increased maintenance cost and reduced growth. The continued locomotion will be in the form of micromovements if more favorable microhabitats are encountered within the same macrohabitat.. If more favorable microhabitats are not encountered within the same macrohabitat, the snails will continue to move into and possibly through another adjacent macrohabitat. They will carry out macromovements. Whenever

environmental conditions induce micromovements or macro-movements these are influenced in rate and direction by the ambient conditions of light and current velocity, as previously discussed. Microhabitats having low food density will contain few snails and the presence of these will be relatively transient. Macrohabitats composed predominantly of such food-poor microhabitats will tend to contain a low density of scattered individuals with few, if any, aggregations formed.

#### Summary - a Listing of the Conclusions

Burrowing is the prevalent, nearly universal response to a penetrable substrate, regardless of light condition or current velocity.

The rate of movement over an impenetrable substrate is related to the type of surface it presents. Movement is steadier and more rapid over a smooth surface than over a more rugged one.

Movement in standing or slowly flowing water is either at random or directed toward food concentrations with gravity, ambient light intensity, and any current velocity having little or no influence.

In moving water of moderate or greater velocity ( $>8$  cm/sec), the rate of movement is greater and the direction of movement is more strongly influenced by the

ambient current velocity and light condition than in standing or more slowly flowing water.

Campeloma exhibits positive rheotaxis not absolutely but rather to an extent dependent upon the ambient conditions of current velocity and light in combination.



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