THE SIGNIFICANCE OF BODY SIZE AND FORAGING MODE IN THE STRUCTURING OF MARINE SOFT-BOTTOM POLYCHAETE ASEMBLAGES

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by

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ABSTRACT

Functional approaches are introduced to study the structure of marine soft-bottom communities. Results of these approaches, based on the feeding type, microhabitat preference, motility pattern and body size of benthic polychaetes, were compared to one based on taxonomy (families). The material came from grab samples collected from the continental shelf and upper slope off the east coast of Canada, in depths of 85 to 622 m ($\bar{x}$=247 m). Various multivariate analyses are used to identify recurrent biological patterns in macrofaunal assemblages. These patterns are then correlated with environmental variables via canonical analysis. No distinct faunal associations are identified from the various approaches. Instead, there was a gradual shift from one type of faunal grouping to another.

The value of each approach in characterizing community structure is evaluated in part by the amount of variation explained by the relationship between the biological and environmental data, and by the statistical significance of this relationship as determined by Monte Carlo tests. The recognition of homogenous groupings of samples based on faunal composition and environmental conditions, however, tends to weigh more heavily in this evaluation. With one exception, all functional and taxonomic approaches show statistically significant patterns. The approach based on feeding microhabitat indicates that this biological attribute of marine benthic polychaetes may not play an important role in the structuring of their communities. The functional approach that comprises all functional attributes (i.e. foraging attributes and

body size) provides the most meaningful ecological characterization of community structure. In this functional approach, groups of samples along the faunal gradients are strongly associated with large-scale topographic features of the Labrador continental shelf and upper slope. Although the taxonomic approach yields similar results, it does not appear to be as efficient in distinguishing between sample points in multivariate analyses. In functional approaches, interpretation of the results in terms of community structure is greatly facilitated by the direct use of ecological attributes such as foraging mode and body size.

About half the variation in the biological data can be explained by variables such as water depth, current regime, sediment grain size and benthic biomasses which are associated with two major environmental gradients extracted by Redundancy Analysis. The effect of other biotic and abiotic factors on benthic community structure is discussed. The remaining variability in the biological data unaccounted for in this study may be explained by these factors, other unidentified processes and noise. The spatial scales at which the biological and environmental data are collected may also influence the outcome of a multivariate analysis and its interpretation.

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I dedicate this ouvrage to my son, Sebastien,

and my daughter, Eve, with all of my love.

May the future offer you as much opportunities

and enjoyment as I have had so far.

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1. INTRODUCTION

A common approach in benthic community ecology begins by making a complete species list with counts for all areas under investigation. With such taxonomic descriptions established, researchers then characterize statistically, with variable success, faunal and/or floral assemblages. These assemblages are often identified as indicators of particular habitats. Examples of this approach can be found in Nesis (1965), Johnson (1970) and Boesch (1973). One school of thought (Petersen 1913; Thorson 1958) regards these associations as a super-organism whose development and distribution are primarily controlled by biological factors (i.e. community in a strict sense; Biernbaum 1974; Hoffman 1978). An alternative school of thought holds that benthic animals are distributed on the basis of physical factors. Here, the concept of discrete communities is rejected since no community boundaries can be detected (Mills 1969; Johnson 1970; Biernbaum 1974; Austin 1985; Wildish 1985). Instead, species associations change constantly as we move along environmental gradients (Austin 1985).

These views, although diametrically opposed, have both contributed to advances in the study of zoogeography and ecology (Sprules and Holtby 1979; Bahr 1982). Taxonomic comparisons of communities from physically similar but geographically distant habitats , however, are usually of little value because of the faunal dissimilarity (Sprules and Holtby 1979), unless information on the feeding ecology of the constituent species is introduced to explain compositional patterns (e.g. parallel communities *sensu* Thorson 1958; see also Josefson 1981, for example). In offshore marine benthic ecosystems, relatively little taxonomic work has been conducted, particularly on small infaunal groups. This situation emphasises the interest in considering other sorts of approaches to study the

structure and ecology of those communities. These and other problems associated with classical taxonomy as used in ecology (e.g. subjective nature of taxonomic classification) are discussed by Bahr (1982).

In the study of community ecology, observed faunistic patterns are taken as indicative of the community structure and can provide new insights into community and ecosystem processes. Regardless of the community concept (i.e. discrete or gradual) one adheres to, it usually assumes some degree of persistance over time (Hoffman 1978). In this context, the community structure is the result of ecological interactions among organisms and between these organisms and the environment. The structure essentially represents an integration of multiple interactions that are characteristic of particular ecological circumstances (Hoffman 1978). Thus the study of community structure assumes that there is a limited number of structural patterns for all possible ecological circumstances and is concerned with understanding the processes leading to the observed patterns.

Ulanowicz and Platt (1985) suggested that a holistic approach might be more appropriate than a strictly taxonomic approach to describe whole-community behavior. The trophic level concept (Lindeman 1942), the community concept (Cody and Diamond 1975; Erwin 1983) and the food web concept (Mills 1975; Pimm 1982), in fact, do appear to be more useful than the traditional taxonomic approach in understanding processes that affect community structure. These concepts, however, require an extensive and usually quantitative knowledge of the biotic and abiotic interactions within the community and may not be appropriate for large natural systems (Cousins 1980, 1985; Platt 1985).

Energy flow within ecosystems is much more dependent upon the body size

and feeding ecology of animals than it is on taxonomic status (Sprules and Holtby 1979; Bahr 1982; Cousins 1985; Platt 1985). Substantial scientific interest has been directed towards the ataxonomic approach based on the body size of organisms (Platt 1985; Calder 1985). Several studies have investigated the size-dependence of physiological processes at the individual and population levels. Peters (1983a) presents a comprehensive review of these so-called allometric relationships and concludes that virtually all aspects of an organism's physiology (e.g. metabolism, growth) are influenced by its body size. At the community level, size structure can play an important role relating to resource availability and use, competition, and predation (e.g. Brooks and Dodson 1965; Peters 1983b; Dickie *et al.* 1987).

Community structure can be characterized in a simple ataxonomic form by the size (biomass) spectrum (Platt and Denman 1978; Platt 1985). While the basic approach was developed by Elton (1927), the size structure of marine pelagic ecosystems was first investigated by Sheldon and Parsons (1967) and Sheldon *et al.* (1972, 1973). Size spectra, characterized by peaks of biomass in specific size classes, have been demonstrated for freshwater pelagic (Peters 1983b; Sprules *et al.* 1983; Sprules and Munawar 1986), marine benthic (Schwinghamer 1981, 1985; Warwick 1984; Gerlach 1985) and terrestrial (Van Valen 1973; Griffiths 1986) communities. These empirical observations have served in the development of theoretical expressions of the body size-abundance relationship in communities (e.g. Kerr 1974; Hall *et al.* 1976; Lynch 1977; Platt and Denman 1977, 1978; Silvert and Platt 1980; Taylor 1980; Platt and Silvert 1981; Calder 1985; Platt 1985; Dickie *et al.* 1987). Cousins (1980, 1985) and Bahr (1982) suggest, however, that a functional approach where the biological data consist of body size and trophic categories would in fact reflect biological

processes in the ecosystem more closely than would body size alone, and certainly much more so than the taxonomic characterization.

In freshwater pelagic communities, Sprules and Holtby (1979) and Sprules (1980) compared the approach using body size and feeding ecology with one based based on taxonomy. They assigned organisms to categories on the basis of body size and feeding ecology. These functional categories were then used instead of the more customary taxonomic categories (i.e. species) in a multivariate statistical analysis. These studies show that results from the functional approach based on size and feeding ecology are ecologically more meaningful than those from the taxonomic approach. In the former, stronger statistical relations were found between zooplankton community patterns and morphometric and hydrological properties of the lakes (see also Sprules and Knoechel 1983). The weakest statistical relation to limnological characteristics was obtained with the taxonomic approach. Sprules and Holtby (1979) conclude that while the latter characterization is of interest in zoogeographic and autecological studies, it does not address the trophodynamics of these planktonic communities.

The objective of the present study is to evaluate the usefulness of the body size/feeding ecology approach for the investigation of marine soft-bottom communities in terms of the interactions between the organisms and the environment. Such an approach, based on the combined use of body size and feeding ecology, has never been applied to benthic communities and may reveal patterns associated with the structure of these communities that are not directly observed through the conventional taxonomic approach.

1.1. Feeding ecology in the benthos

Hunt (1925) was one of the first marine ecologists to assign benthic

macrofaunal organisms to trophic categories such as deposit feeders, suspension feeders and carnivores. These categories were subsequently recognized for their significant contribution to community structure by Sanders (1958, 1960), Rhoads and Young (1970), Pearson (1971), Wildish (1977, 1985), Commito and Ambrose (1985) and Wilson (1986), among others. The distribution and abundance of benthic invertebrates in those trophic categories are affected by environmental factors such as water depth, sediment properties and water currents (e.g. Bloom *et al.* 1972; Jumars and Fauchald 1977; Biernbaum 1979; Dauer *et al.* 1981; Maurer and Leathem 1981; Whitlatch 1981; Jumars and Nowell 1984; LaBarbera 1984; Wildish 1985).

Detailed studies of the feeding ecology of marine benthic invertebrates have been conducted only for a limited number of macrofaunal taxa. My study addresses the polychaetous annelids, usually the dominant group in both abundance and biomass among macrofaunal organisms found on soft-bottoms (Sanders 1958; Maurer *et al.* 1976, 1982; Massad and Brunel 1979; Maurer and Leathem 1980). Compared to the situation in other important benthic invertebrate groups (e.g. molluscs and crustaceans), a substantial amount of information on the feeding ecology of polychaetes is available from the literature, and has been reviewed and summarized by Jumars and Fauchald (1977) and Fauchald and Jumars (1979).

Fauchald and Jumars (1979) defined a series of feeding guilds based on feeding modes (macrophage and microphage) and submodes (herbivore, carnivore, suspension-feeder, surface deposit-feeder and subsurface deposit-feeder), motility patterns (sessile, discretely motile and motile) and morphological features of the feeding apparatus (unarmed pharynx, jawed pharynx and tentaculate mucous device). This classification has been used by

Maurer and Leathem (1981) and Gaston (1987) to study polychaete assemblages on the middle Atlantic continental shelf. Their results clearly support the contention that the distribution and abundance of soft-bottom invertebrates are, to a great extent, dependent upon their feeding ecology which in turn is affected by environmental factors.

Multiple limiting factors control the distribution of marine macrobenthic animals (Wildish 1985). Among these factors, sediment properties and sediment dynamics have a major influence on the polychaete distribution by interacting with their feeding ecology (Fauchald and Jumars 1979; Jumars and Nowell 1984). In soft bottoms, sessile polychaetes are generally associated with more stable sediments encountered primarily in deep waters while motile, carnivorous polychaetes are relatively more abundant in shallow waters, on coarser sediments (Maurer and Leathem 1981; Gaston 1987). Deposit-feeders and suspension feeders are found in most soft-bottom habitats but are usually more abundant in areas with high sediment carbon content and water-column production.

In the present study, the feeding ecology of benthic polychaetes, hereafter referred to as **foraging mode**, is based on three foraging attributes: **feeding type** and **motility pattern** which are equivalent to Fauchald and Jumars' feeding mode and motility pattern, and **feeding microhabitat** (water column, sediment surface and sediment subsurface). Three aspects of my classification differ from Fauchald and Jumars' scheme. Firstly, herbivores and carnivores are grouped under the feeding type **macrophage** since polychaetes are seldom true herbivores or carnivores but frequently use a mixed diet, depending on the environmental circumstances (Fauchald and Jumars 1979; see also Gaston 1987). Also, in waters deeper than 100 metres, herbivory is expected to be rare,

especially if sampling is conducted during periods of low surface primary production (Fauchald and Jumars 1979; Maurer and Leathem 1981; Gaston 1987). Secondly, all detritivores (suspension-feeders and deposit-feeders) are grouped under the feeding type **microphage** since, in most cases, the distinction between the origin of their food (i.e. freshly-settled seston or resuspended detritus) is unclear (Fauchald and Jumars 1979). Instead, **microphages** and **macrophages** are distinguished on the basis of the **microhabitat** from which they extract their food. Finally, morphological features of the feeding apparatus (Fauchald and Jumars 1979) are not included in this classification. This attribute was found to be less useful than the other foraging attributes (Gaston 1987) and is generally found to be strongly correlated with **feeding type** and **microhabitat**.

1.2. Body size and benthic community structure

The size distribution of benthic organisms in deep-sea communities has been discussed in general terms by Thiel (1975). His major conclusion was that, with increasing depth and decreasing food supply, the average size of the macro- and meiofauna decreases. Schwinghamer (1985) found, however, that any tendancy to shift peaks and troughs in size spectra toward smaller sizes can be explained by sediment granulometry alone (see also Polloni et al. 1979).

Schwinghamer (1981, 1985) elaborated size spectra for several marine soft-bottom communities which are characterized by three distinct biomass peaks. These peaks correspond to the ecological grouping of organisms into microfauna (grain-surface dwellers of size range 0.5-8 μm equivalent spherical diameter, or ESD), meiofauna (interstitial organisms of 8-500 μm ESD) and macrofauna (macroscopic surface-dwellers and burrowers of size greater than 0.5-1.0 mm ESD). According to Schwinghamer (1981), this structure reflects ecological

processes in the benthos that are different from those in pelagic communities. While highly conservative over a wide range of environmental conditions, the exact location of the peaks and troughs of biomass is determined by sediment properties (Schwinghamer 1985). It is argued that sediment properties (e.g. particle size, stability, compactness/water content) place certain constraints on the body size of interstitial and burrowing organisms. When the size distribution is expressed as a function of the number of species instead of biomass, however, sediment properties do not appear to affect the position of peaks and troughs (Warwick 1984). This suggests that, in addition to ecological constraints associated with the life in sediment (e.g. grain size, pore size, sediment stability), there are evolutionary implications dependent on the availability of niches. Biomass troughs may represent regions of the size spectrum where phyletic shift and a shift in the predominance of life-style co-occurs (Schwinghamer 1985).

While the size spectrum approach appears to be attractive to study community structure (Platt 1985), its application to groups with a limited overall size range, such as macrofaunal polychaetes, may not be as informative. Still, the size-dependence of ecological interactions among benthic organisms (e.g. competition, predation, resource partitioning) and between these organisms and the environment (i.e. environmental constraints on size by factor such as sediment granulometry and stability and near-bottom currents) has clearly been demonstrated by Paine (1974, 1976), Schwinghamer (1983) and Warwick *et al.* (1986), among others. Therefore, in this study, the body size of macrofaunal polychaetes will be used as an attribute of each individual specimen in a functional approach similar to the one used by Sprules and Holtby (1979) for pelagic communities (see pages 3-4).

1.3. Scope of study and hypotheses

From the previous considerations, it is apparent that body size and foraging mode are important biological attributes that contribute to the structuring of communities. These attributes are affected by environmental factors such as sediment properties. Therefore, we can assume that the distribution and abundance of soft-bottom macrofaunal organisms are, at least in part, the result of this biotic-abiotic interaction. In fact, we can expect this interaction between the functional attributes and the environment to be more important (i.e. more direct effects) than the one between taxonomic categories and the environment. Therefore, a characterization of benthic communities based on body size and foraging mode should show stronger statistical relationships to the environmental variables than the conventional taxonomic characterization. In this study, the latter will consist of a classification of polychaetes to family. Heip *et al.* (1988), Warwick (1988) and Ferraro and Cole (1990) have demonstrated that multivariate analyses of family data show no significant loss of information, and often provide a better separation of the samples, in comparison with analyses based on species data.

In addition to comparing the functional approach based on body size/foraging mode to the taxonomic approach, the importance of each foraging attribute (feeding type, feeding microhabitat and motility pattern) and body size will also be examined separately. From this, it may be possible to assess the contribution of each biological attribute to the structuring of the soft-bottom polychaete assemblages under study. Here, it is assumed that the degree to which an attribute contributes to the structure of a community is a function of the relationship between the distribution of that attribute among the samples and the environmental variables characterizing those samples (see Green and Vascotto 1978; Sprules and Holtby 1979).

Based on the functional and taxonomic approaches, the following predictions can be made concerning statistical relationships between the biological data and the environmental variables:

- A significant relationship exists between the biological and environmental data in a functional approach based on the body size and/or foraging attributes.

If this prediction is supported, then the following predictions can be made:

- A stronger relationship is found between the biological and environmental data when both body size and foraging mode are included in the functional approach than when only one attribute is included.
- The 'significant' functional approach shows an equal or better relationship (as indicated by a greater multiple correlation coefficient) to the environmental variables than does the taxonomic approach, assuming that the latter is significant.
- Sediment grain size accounts for a significant portion of the variation in the biological data, either in a functional or a taxonomic approach.

If the significance of body size and foraging attributes in explaining the compositional patterns of marine soft-bottom polychaete assemblages is demonstrated, then the functional approach can be used to examine the structure of benthic communities. Ultimately, it might be possible to predict the functional composition of particular soft-bottom habitats from the knowledge of a number of important environmental variables.

1.4. Analytical techniques

In the context of this study, two aspects of the comparisons of functional and taxonomic approaches could affect the choice of an appropriate multivariate statistical method. On the one hand, the change in faunal composition over the sampling range can be expected to be rather small (i.e. short biological gradient). Unlike the classical approach where species composition often changes completely between extreme sampling sites (i.e. complete turnover of communities), in a functional approach most attributes (e.g. body size classes, feeding types, etc.) will probably always be represented by at least some individuals; it is the proportion of individuals among those attributes that will change. The same argument probably holds true for the taxonomic approach based on families. Under this circumstance, ordination and classification techniques that are known for their ill-performance with short gradients (Jongman *et al.* 1987) will probably be inadequate. A second implication of this short-gradient change in biotic composition is that changes between samples, even over a wide range of environmental conditions, may be subtle ones. Hence, discrete assemblages or groupings of samples may not be distinguishable by ordination and clustering techniques.

On the other hand, the various functional approaches and the taxonomic approach will involve a different number of variables per analysis. In all ordination techniques, the proportion of variation in the data that is accounted for by each axis is strongly dependent on the initial number of biological attributes in the data matrix. Therefore, the comparison of the results in the form of proportions of variance accounted for by each axis (in eigenanalysis) or stress values (in Multidimensional Scaling) may be greatly hampered.

Various numerical methods have been introduced for the analysis of faunal

composition and its relationship to environmental factors. In an exploratory analysis of ecological data, it is assumed that the strength of this relationship is a direct measurement of the degree to which environmental factors control the biological parameters *in situ* (Green and Vascotto 1978). In order to assess which methods are appropriate to address the predictions as well as the problems presented above, a review of the major multivariate techniques is necessary. Reviews of methodology can also be found in Biernbaum (1974), Clifford and Stephenson (1975), Green and Vascotto (1978), Field *et al.* (1982), Kershaw and Looney (1985) and Jongman *et al.* (1987), among others.

Most multivariate methods designed for the analysis of survey data follow one of two approaches: (1) the biological data are summarized onto fewer variables (i.e. axes or factors) which are then interpreted in terms of the environmental data via a univariate or multivariate regression procedure (indirect gradient analysis, *sensu* Whittaker 1967), or (2) the biological and environmental data are summarized simultaneously, but summarization of the biological data is constrained by the environmental data (e.g canonical ordination, ter Braak 1986; direct gradient analysis, *sensu* Whittaker 1967). Ordination and clustering techniques are used to summarize the data by extracting dominant patterns or groupings. The choice of a specific technique, however, may depend on the model which is assumed to underlie the data distribution (i.e. linear, Gaussian or monotonic), or the robustness of the technique (Green and Vascotto 1978; Gauch 1982a), but it may even be arbitrary (e.g. dependent on accessibility).

Sprules (1977) describes a statistical procedure which he subsequently applied in the body size/feeding ecology approach to study limnetic zooplankton communities (Sprules and Holtby 1979). In this procedure, Principal

Components Analysis (PCA) reduces the original sample-by-species matrix to a sample-by-axis (factor or component) matrix where the number of axes is less than the number of species. In a graphic form, the 'reduced' data is displayed on two or more axes where samples with similar species composition are found closer to each other than are dissimilar samples. A stepwise multiple regression analysis is then performed between the 'reduced' biological data and the environmental data (Sprules and Holtby 1979) in an attempt to interpret patterns in community structure. Environmental factors which have the greatest correlation coefficient with the 'reduced' biological data are considered to have the greatest influence on community structure.

A similar approach taken by Biernbaum (1974, 1979) to study the structure of benthic amphipod assemblages uses Principal Coordinates Analysis (PCO) instead of PCA, and the Spearman rank correlation coefficient instead of multiple regression (see also Sprules 1977). While both PCA and PCO are metric procedures, PCO makes no parametric assumptions and is more appropriate for analyses where the number of samples is smaller than the number of species (Clarke and Green 1988).

Another metric ordination technique, Detrended Correspondence Analysis (DCA), is based on a Gaussian unimodal curve model instead of the linear model of PCA (Hill and Gauch 1980). DCA appears more robust than the other techniques (Gauch 1982a; Peet *et al.* 1988), particularly when there are a large number of zero counts in the data and more attributes than samples (i.e. not hampered by problems of multicollinearity). Two major changes were introduced to DCA from the original Correspondence Analysis: (1) an attempt to remove the 'horseshoe effect', a curved configuration of the points on a two-dimensional ordination, which is typical of all other ordination techniques, and (2) rescaling

axes so that equal distances in the ordination correspond to equal differences in species composition. Advantages and disadvantages associated with the changes are discussed by Wartenberg *et al.* (1987) and Peet *et al.* (1988). Because this technique is based on a Gaussian (bell-curve) model, it is not recommended for data where short gradients are expected (Jongman *et al.* 1987).

These ordination techniques are all based on the eigenanalysis of principal components and differ mostly according to the type of transformation and standardization applied to the data. A program introduced by ter Braak (1986), called CANOCO (Canonical Community Ordination), performs these metric ordination techniques and also includes a canonical procedure for most of them. Unlike canonical correlation analysis, which is limited to a number of species (biological variables) less than n-q (where n is the number of samples and q is the number of environmental variables), the canonical techniques included in CANOCO can analyse any number of species.

Another strategy was proposed by Field *et al.* (1982) to analyse multispecies distribution patterns. It uses a nonmetric equivalent of PCO, Multidimensional Scaling (MDS), which operates from similarity/ dissimilarity data (like PCO) and uses a less restrictive monotonic model for the data distribution onto underlying gradients. This technique is able to handle data matrices with large numbers of zero counts and more attributes than samples. Further discussion of this technique can be found in Shepard *et al.* (1972), Gauch *et al.* (1981) and Clarke and Green (1988). Field *et al.* (1982) recommend a clustering analysis of the biological data to confirm patterns observed in the MDS analysis. The patterns are then related to the environmental variables using a visual overlay of categories for each environmental variable on the ordination. Clarke and Green (1988) provide a statistical test of the relationship between the 'reduced' data

and the environmental variables, using a multivariate analysis of covariance and permutation/randomization tests.

Finally, in their brief review of multivariate methods, Green and Vascotto (1978) object to the use of PCA and other ordination techniques for derivation of axes which are to be interpreted as environmental factors. They argue that while ordination procedures are useful for graphical display of the data, important problems arise from the restrictiveness of assumptions underlying the distribution model (i.e. linear, unimodal and even monotonic) and the presence of the 'horseshoe effect' (except in DCA). Green and Vascotto (1978) recommend using a clustering method which makes no assumptions at all to characterize homogeneous biotic assemblages. These assemblages are then considered as groups in a Canonical Discriminant Analysis on the environmental variables. This procedure still assumes a linear combination of the environmental variables in the discriminant analysis, with the assumptions of a linear multivariate analysis (i.e. independence of samples, multivariate normal distribution and homogeneity of covariances matrices). It also assumes that distinct biotic assemblages can be recognized from the clustering analysis.

The multivariate methods described above will usually yield similar results and are considered to be robust (i.e. results are not strongly affected by violations of assumptions associated with the underlying statistical model). Unfortunately, no methods can fully address the problem posed by the comparison of approaches with unequal numbers of biological variables. Nevertheless, as recommended by Clarke and Green (1988), the statistical procedure used in the study will combine methods of classification and standard/canonical ordination to identify and confirm community patterns and to see if the predictions are borne out.

The classification technique UPGMA will be used to show coarse patterns which can be compared with those displayed by ordination techniques. Like most clustering methods, UPGMA makes no assumption about the underlying statistical distribution of the data and has been shown to be appropriate for ecological data matrices with many zero counts such as those of the present study. The versions of MDS and PCA used in this study can also handle this type of data matrix wherein the number of species (i.e. biological variables) exceeds the number of samples (i.e. cases). These ordination techniques are based on two different underlying statistical models (monotonic and linear, respectively) which would fit 'short-gradient' data. The fact that the underlying models are different may also help detect and reject sporadic patterns.

Based on the same robust iterative algorithm as the above PCA, Redundancy Analysis (RDA) will be used to examined the relationship between biological and environmental data (ter Braak 1986). Like PCA, RDA is an eigenanalysis that provides directly the proportion of variance explained in the biological data by each axis or factor. These values will be used for comparisons of approaches with a similar number of variables.

2. MATERIALS AND METHODS

2.1. Benthic sampling and initial treatment

The survey area consisted of two regions off the east coast of Canada, the Labrador continental shelf and upper slope and the Hermitage Channel to the south of Newfoundland (Figure 1). A 0.1 m^2 van Veen grab was used to obtain 33 benthic samples from the Labrador shelf and slope (Table 1) in October 1983, during the C.S.S. Hudson cruise 83-030. The geographic range of the sampling sites extends from Hudson Strait (61°33'N) to Belle Isle Bank (52°42'N, Figure 1) in water depths of 85 to 622 m ($\bar{x}$=247 m). In the Hermitage Channel (47°29'N, 56°25'W), three Van Veen grab samples were collected from station HC13 (305-375 m depth; Table 1) during *C.S.S Dawson* cruise 84-040, in December 1984.

A subsample of surface sediment was extracted from each grab sample for sediment grain size analysis. The remainder of the sediment was sieved onto a 420 μm mesh to extract macrofaunal organisms. These were fixed in 4% buffered formaldehyde and later transferred into 70% ethanol for processing in the laboratory. Macrobenthic organisms were sorted to major taxonomic groups (e.g. Foraminifera, Nematoda, Polychaeta).

2.2. Determination of polychaete foraging mode and body size

2.2.1. Foraging modes

Each polychaete was examined under a Wild-M5A dissecting stereomicroscope and classified to family. The **foraging mode** was then determined, following the scheme described below. Identifications to family, or when necessary to lower taxonomic levels (Fauchald and Jumars 1979), were used to define the **foraging mode** in terms of three attributes: the **feeding type**, the **feeding microhabitat**, and the **motility pattern** (Table 2).

Two **feeding types** are recognized on the basis of food particle size and handling method (Fauchald and Jumars 1979). The **macrophage feeding type** includes herbivores, carnivores, and scavengers; food particles are handled singly, or at most only a few at a time. The **microphage feeding type** comprises suspension feeders and deposit feeders which handle food particles in bulk. The **feeding microhabitat** defines where, in a vertical sense, the polychaetes feeds: **water column**, **sediment surface**, or **sediment subsurface** (Fauchald and Jumars 1979). In addition to these three basic strata, some taxa will obtain their food from both the **water column** and **sediment surface**.

Jumars and Fauchald (1977) defined three **motility patterns** that relate to feeding: **sessile**, **discretely motile**, and **motile**. **Sessile organisms** do not move sufficiently through their lifespan to feed in an area appreciably different from the one in which they settled as larvae. **Discretely motile organisms** are capable of moving between periods of feeding, but are immobile during food uptake. **Motile organisms** move independently of the use of the feeding apparatus or may even require movement for efficient feeding (Fauchald and Jumars 1979).

2.2.2. Estimation of body size

Measurements were taken using a digitizing system similar to the one described by Roff and Hopcroft (1986), although independently developed. Individual polychaetes were examined under a stereomicroscope fitted with a *camera lucida* which projected an image on a digitizing tablet. Details of the hardware, software, and operation of the measuring apparatus are presented in Appendix A. Individual volumes (V) were estimated by measuring the total length and maximum diameter of each specimen. It is assumed that the shape of

all polychaetes is best described by a prolate ellipsoid, and therefore with the volume

$$V = 2/3\,(\pi L r^2), \qquad \text{(Eq. 1)}$$

where L is the length and r is the radius of the ellipsoid. When the maximum diameter, d, is used in place of r, equation 1 becomes

$$V = 1/6\,(\pi L d^2). \qquad \text{(Eq. 2)}$$

In the following analyses, volumes were converted into equivalent spherical diameter (*ESD*), where

$$ESD = 2\,(3V/4\pi)^{1/3}, \qquad \text{(Eq. 3)}$$

to allow comparison with published data (see Schwinghamer 1981). This standardization has the further advantage of transforming the data from a strongly skewed-to-the-right distribution to a normal distribution.

In many instances, polychaetes were broken during collection and extraction from the sediment. In such cases, only a partial body length and the maximum diameter could be measured from the anterior portion of the animal (tail portions were of little use for they bore no identifying features). To circumvent the problem of underestimating the total body volume from incomplete specimens, the total body length was estimated by the following graphical method:

The observed length of all specimens from a given taxonomic unit (i.e. family, subfamily, or genus) was plotted against the measured maximum diameter of the specimen. For a given diameter, complete specimens display the highest length/diameter ratio while truncated specimens have smaller values, depending on the degree of truncation. The total length/maximum diameter relationship was assumed to be linear and was estimated by visually fitting a straight line through the bulk of points representing specimens with the largest length/diameter ratio (Figure 3a; see also Appendix B). Specimen lengths which

were, for a given diameter, clearly below the range of points surrounding this estimated 'average' total length (i.e. below the dashed line in Figure 3) were adjusted to that 'average' length. The range, and consequently the position of the cutoff (dashed) line, was determined from qualitative observations on the proportion of truncated specimens in each taxon. Therefore, the position of the fitted lines varies with the degree to which a taxon is prone to truncation. For example, specimens of the families Cirratulidae and Spionidae (Figure 3b and c, respectively) were badly truncated and the fitted lines were placed close to the upper margin of the cloud of points. Taxa that show little tendency to truncate (e.g. Nephtyidae, Opheliidae, Pectinidae, and Polynoidae) demonstrate a fairly strong linear relationship between total body length and maximum diameter.

2.3. Environmental data

The variables used to describe the physical environment at the sampling sites are listed in Table 3. Values for these environmental variables at each site are presented in Appendix C. Station latitude was expressed on a decimal scale where 40° and 60° equal 0 and 2000, respectively. Distances were measured from navigation charts (scale 1:50000) between the sampling site and the nearest 0 (shore), 200 and 2000 m isobaths. Proportions (in weight) of clay, silt, sand, and gravel in the sediment from each sample were calculated from the grain size analysis, using a sedigraph (Labrador samples) or a settling tube (Hermitage Channel) for the mud fraction, a settling-tube for the sand fraction, and dry sifting for the coarser fraction (Buchanan 1984).

Annual averages and ranges in water temperature and salinity were estimated from data collected between 1928 and 1979 for the Labrador continental shelf and slope and summarized by Lazier (1982). Annual averages were calculated from monthly averages at 50, 100, 150, and 200 m (Lazier 1982:

Figure 6). Mathematical functions were fitted through the annual averages and the offshore average (at approx. 1000m; Lazier 1982: Figure 3). The latitudinal variation in average temperature was estimated from regression equations (Lazier 1982: Figure 7). Values of average temperature, $\overline{T}$, average range in temperature, $\Delta\overline{T}$, average salinity, $\overline{S}$, and average range in salinity, $\Delta\overline{S}$, at each sampling site were estimated from those derived functions (Appendix D), where

$$\overline{T} = -0.42 + \frac{4.42}{1 + 245e^{-0.002 + Depth}} + 0.0018\,Latitude - 2.17, \qquad \text{(Eq. 4)}$$

$$\Delta\overline{T} = 5 + 2\cos\left(\frac{\pi}{475}(Depth + 200)\right), \qquad \text{(Eq. 5)}$$

$$\overline{S} = 2.20\,(15.77 - e^{-0.005Depth}), \text{ and} \qquad \text{(Eq. 6)}$$

$$\Delta\overline{S} = 2.33 + 0.70\cos\left(\frac{\pi}{750}(Depth + 500)\right). \qquad \text{(Eq. 7)}$$

Records of current velocity from the Labrador shelf and upper slope are relatively scarce. Fissel and Lemon (1982) described four circulation regimes based on a review of data collected prior to 1981:

1. Unsteady flows, with weak vertical shear and moderate energy, associated with stations located on the Banks of the continental shelf.
2. Unsteady flows with high energy, and moderate vertical shear, found at locations in Saddles (between banks).
3. Stations with flows which are relatively strong and steady, but less so than (4), and which appear to have a large vertical shear, associated with locations in the Marginal Trough.
4. Strong, very steady flows and moderate vertical shear, associated with locations at or near the continental shelf break.

The current regime at each sampling site was coded from weak (1) to strong (4), following the above classification except where sites were located between two geographic areas defining two different regimes. In such cases, a half point value was added or substracted to account for boundary effects (see Appendix C).

For the station in Hermitage Channel, data on temperature and salinity (Table 3) were reported by Hay and de Young (1983). The water current regime was estimated from indirect information on bottom photographs (i.e. sediment texture, behaviour of camera frame, and movement of sediment particles after resuspension). Finally, the total biomasses of macrobenthic invertebrates and polychaetes from each sample were reported by Hutcheson *et al.* (1985) and are included with the environmental data (Table 3).

2.4. Statistical analyses

In order to evaluate the relative importance of each biological attribute (i.e. feeding type, feeding stratum, motility pattern, body size, and taxon) in community structure, the raw data for each individual (foraging mode, body size, and taxonomic group) were converted into six different approaches: feeding type (**FE**), feeding microhabitat (**MI**), motility pattern (**MO**), body size (**SZ**), combined foraging mode and body size (**FORASZ**) and taxon (**TX**). Within an approach, each variable (column) represents the absolute frequency of polychaetes in a given sample (row) that are in the same category for the attribute, or for combined attributes. Unlike body mass (i.e. biomass per category), polychaete abundances can be more informative in situations where a large number of small individuals have recently settled, as is often the case after a disturbance. The importance of body size is evaluated in the functional approaches **SZ** and **FORASZ**. All possible combinations of foraging attributes (Table 2) produce ten

foraging modes (Figure 2). Therefore, most modes include at least two families. The exception is the family Sabellidae; the subfamilies Sabellinae and Fabricinae display two different modes, and the Fabricinae are exclusive as to the mode microphage/water column/discretely motile. This functional classification is clearly not a simple reclassification based on taxonomy. In fact, at least seven families are characterized by two foraging modes (Appendix Table F-1). Therefore, one cannot predict the functional category from simply knowing the family.

Body size was expressed in size classes on a logarithmic base 2 scale. Six size classes were used in the approach **SZ** with the intervals ESD < 0.5 mm, 0.5 mm $\leq$ ESD < 1.0 mm, 1.0 mm $\leq$ ESD < 2.0 mm, 2.0 mm $\leq$ ESD < 4.0 mm, 4.0 mm $\leq$ ESD < 8.0 mm, and ESD ≥ 8.0 mm. In the approach **FORASZ** (Figure 2), four size classes were use to limit the resulting number of variables: ESD < 1.0 mm, 1.0 mm $\leq$ ESD < 2.83 mm, 2.83 mm $\leq$ ESD < 8.0 mm, and ESD ≥ 8.0 mm. While this approach yields a number of variables (i.e maximum of 40 functional categories) comparable to the one obtained in the taxonomic approach, there is no direct correspondance between those two sets of variables. As previously indicated, a given functional category does not correspond to a family in particular but rather to a group of organisms within a given size range which usually represent two or more families.

Each approach was subjected to the following analytical procedure. The absolute frequency (i.e. number of individuals per sample) was standardized to relative frequency (%) of individuals per variable within each sample. In subsequent analyses, this standardization serves to remove the differences in total abundance between samples (Sprules 1977). Transformations (normalization) were applied to the data so that the distribution meets the

assumptions of approximate normality and of equitability of variance among samples (Clarke and Green 1988). As recommended by Field et al. (1982) and Warwick (1988), a 4th root (√√) transformation was applied to the unstandardized (abundance) data, thus scaling down the influence of numerically abundant variables. Analyses based on abundance data address biological patterns associated with among-sample variation in total abundance. Normalization of standardized (percentage) data is usually done with an arcsin-square root transformation (Sprules 1977; Sokal and Rohlf 1981). I also used a logarithmic transformation ($\log_e[x+1]$) which was introduced by Aitchison (1983) for a specific Principal Components Analysis procedure (see below). This method corrects problems of curvature in the configuration of ordination points (i.e. "horseshoe effect").

Transformed data (unstandardized and standardized) were submitted to the clustering method UPGMA and to two ordination techniques, Multidimensional Scaling (MDS) and Principal Components Analysis (PCA), to extract dominant community patterns. The hierarchical classification technique UPGMA, an unweighted pair-group method with arithmetic averages, was used to define clusters of samples which are represented by distinct faunal assemblages. This technique is based on a polythetic agglomerative clustering strategy and is the most frequently used in ecology (Gauch and Whittaker 1981). Classical non-metric MDS and UPGMA were used with the Bray-Curtis measure of similarity applied to the √√-transformed (abundance) data and the arcsin√-transformed (percentage) data. This index, which was found to be robust (Field *et al.* 1982) and accurate (Bloom 1981) has the form

$$\delta_{jk} = \frac{\sum_{i=1}^{s} |Y_{ij} - Y_{ik}|}{\sum_{i=1}^{s} (Y_{ij} + Y_{ik})}$$

where Y_{ij}= score for the ith variable in the jth sample, and Y_{ik}= score for the ith variable in the kth sample.

Sample classifications (i.e. normal or q-analysis) by UPGMA and MDS were performed with the statistical package NTSYS. Goodness of fit of MDS ordination to the original data is estimated by the stress statistic. Values of stress range between 0 and 1 and usually, those less than 0.3 are indicative of fair to excellent (stress < 0.1) fit (Rohlf 1988). Groupings from UPGMA are represented by envelopes around sample points on the MDS ordination.

Analyses of unstandardized (√√-transformed) data by PCA were centered by species (i.e. ordinary PCA; ter Braak 1986) while those with standardized (log-transformed) data involved double centering by species and samples (i.e. double centered PCA; Aitchison 1983). In all PCA's, species (i.e. biological variable or family) and sample points are displayed on the same ordination diagram. Biological variables which contribute most to the separation of samples are displayed at the periphery of the ordination diagram while those that are located at or near the origin of the diagram are undifferentiated by the axes. Only the former will be labelled in the diagrams.

Correlations between biological patterns extracted by PCA and the environmental variables were examined directly with a canonical procedure associated with PCA in the computer programme CANOCO . Redundancy Analysis (RDA, also called Canonical Principal Components Analysis; ter Braak

1986) is essentially a constrained PCA which, as an eigenvector ordination technique, identifies underlying dimensions (factors) in the biological data that are linear combinations of the standardized environmental data. In other words, the configuration of points (species or other biological attributes, and samples) along each ordination axis, and consequently the amount of variation in the biological data explained by the axes, is constrained at each iteration by a linear relationship (i.e. multiple regression) between each axis and the standardized environmental variables. Within CANOCO, the environmental variables are also examined for occurrence of multicollinearity. Environmental variables with values of $R^2 > 0.90$ (i.e. variables that can be predicted from a multivariate linear relationship among the other variables) were excluded from the canonical analysis (see Table 3).

Results of RDA can be expressed in terms of amount of variation in the biological data that is accounted for when each axis satisfies the constraint of linear combination with the environmental variables. The statistical significance of the eigenvalue (i.e. proportion of variance explained) for the first axis and the sum of eigenvalues for all axes (i.e. trace) was evaluated within CANOCO by permutation/randomization (Monte Carlo) tests. Here, the environmental data are randomly linked to the biological data by permuting the sample numbers. For each functional and taxonomic approach, RDA was performed 500 times to determine the level of significance. These tests have the advantage of making no assumption about the statistical distribution underlying the relationship between the biological and environmental data.

The graphical representation of RDA is a biplot of "species" (or biological categories) and sample ordinations, with superposed arrows (vectors) representing environmental variables. The coordinates at each arrow head

correspond to the biplot scores of an environmental variable. The direction and extent of an arrow can be interpreted qualitatively as approximate covariance between biological and environmental variables (ter Braak 1986). Arrows which are at 90° angle from each other represent independent environmental variables while those that are more or less parallel share the effect on the biological data. The same rule applies for the relationship between a biological variable or a sample point and the environmental variables.

The absolute length of environmental arrows among biplots, however, is arbitrary. A scaling factor is applied to environmental biplot scores in order to display them on the same scale as the biological variable and sample plots. Nevertheless, the relative contribution of each environmental variable to the statistical relationship with any given biological variable or sample in the ordination can be estimated by projecting each arrow (environmental variable) perpendicularly onto the biological variable or sample vector (i.e. straight line passing through the origin and the coordinates of the point). In other words, environmental variables which have a longer projection onto the biological vector are more strongly correlated with that biological variable or sample and therefore, more closely related to the pattern of community variation shown in the ordination. Further details on the biplot method can be found in ter Braak (1983, 1986). The comparison of the functional and taxonomic approaches will be based on both the amounts of variation explained and the two-dimensional graphic representations.

3. RESULTS

3.1. Sediment granulometry

Results of the sediment analysis for all samples used in this study are summarized in Figure 4. Most samples have sediments which appear along the sand-mud axis, with some gravel content. Five samples are from sites with coarse sediment (sandy gravel). The sand-mud axis can be divided into three equal segments: Muddy samples come from deep-water sites, whether near Hudson Strait, in the Marginal Trough south of Nain Bank (latitude 56°N), or from Hermitage Channel (Figure 1); Sandy samples tend to come from sites near the edge of the banks or of the marginal trough (depth around 200m, 8 out of 12 samples); Sandy-muddy sediments are mostly from shallow-water sites on the banks or near shore (6 out of 9 samples). Finally, sandy-gravelly samples (i.e. samples 4, 24, 40, 78, and 89; Figure 1) and samples with some gravel content (i.e. samples 3, 30, 87, and 79) often come from deep-water sites (depth > 200m; 6 out of 9 samples).

3.2. Functional and taxonomic approaches

The comparison of functional and taxonomic approaches, whether qualitative or quantitative, can only proceed once ecological patterns from each approach have been identified. In the following sections, each approach is examined by comparing results from the different numerical methods to identify recurrent patterns. Analyses performed with abundance (unstandardized) data and with percentage (standardized) data are considered separately.

A total of 7728 polychaete worms were examined in this study. The number of individuals varied considerably among samples, ranging from 5 to 947 worms. Most samples (83.3%) contained less than 500 individuals, with an overall

average of 215 worms per sample (see Appendix C). Because of this large variation in the total number of polychaetes among samples, a primary pattern (gradient) extracted by analyses with abundance data corresponds to the total abundance gradient. Once identified for the first approach, emphasis will be directed toward subsequent gradients which are represented particularly by analyses of percentage data.

3.2.1. Feeding type approach

Abundance data

The vast majority of samples examined in this study are dominated by microphagous polychaetes (Figure 5; see also Appendix C); only 8% of the samples (3 out of 36) contain more than 50% of macrophages. After transformation (Figure 6), the primary gradient expressed in the bivariate plot corresponds to that of the total abundance. Classification of samples by UPGMA (Figure 6) produces groupings which coincide with this gradient. Since this approach contains only two variables, ordinations from Multidimensional Scaling (MDS; Figure 7) and Principal Components Analysis (PCA; Figure 8) are essentially identical to the bivariate plot (Figure 6). In PCA, however, axes are orthogonal and, therefore, the primary gradient in the biological data is represented parallel to the first axis. In the PCA ordination, the biological variables (macrophage and microphage in Figure 8) are represented on the right-hand side where both variables show high abundances coinciding with high total abundances. The second gradient, along Axis 2, corresponds to variation in proportions between macrophages and microphages. This gradient is essentially equivalent to the first one extracted by analyses based on percentage data (see next section).

The relationship between the ordination of samples and environmental

variables is shown by the Redundancy Analysis (RDA; Figure 9). The primary difference between the RDA biplot and the PCA ordination (Figure 8), other than the presence of arrows representing the direction and extent of statistical relationships between biological and environmental data, is the change of orientation in Axis 1. This is arbitrary and does not affect the results.

Samples with high abundance of polychaetes (left-hand side of Figure 9) are correlated with high total biomass and great distances from the 2000m isobath. These samples are also negatively correlated with environmental variables such as water depth, latitude, predicted average temperature, and sediment clay content (i.e. arrows oriented away from these samples; Figure 9). In other words, most high-abundance samples tend to be found in shallow water, particularly in the southern part of the study area (Figure 1), where current regimes are weak and sediments are mostly sandy (i.e. negatively correlated with clay and gravel; Figure 9). Conversely, samples with low abundance of polychaetes tend to be from deep-water sites, several of which are located in the northern part of the study area (i.e. five samples from the vicinity of Hudson Strait; Figure 1). Current regimes at these sites are usually strong while bottom sediments are fine. There does not seem to be any strict relationship between assemblages (based on abundance among feeding types) and large-scale topographic features of the Labrador shelf such as banks, saddles and the Marginal Trough.

Variation over the second axis, which is associated with differences in proportion between macrophages and microphages, is strongly associated with the polychaete biomass, and to lesser extent to silt and gravel content in the sediments (Figure 9). Further description of this relationship is presented below, when examining results from analyses based on percentage data. The total

proportion of variance in the abundance data explained by the environmental variables is about 61% (Table 4), leaving approximately 39% of the variance unaccounted for by environmental variables (Figure 10).

Percentage data

As indicated previously, once the effect of total abundance among samples is removed, the remaining gradients to be extracted usually represent differences in the proportion between the various biological variables. In the feeding type approach, since there is only two variables, differences in proportion are expressed over only one gradient which is a simple linear function (i.e. Y= 100 - X; Figure 11). This gradient is extracted by MDS (with a curvilinear distortion; Figure 12), UPGMA (Figures 11 and 12) and PCA (Figure 13).

The relationship between sample ordination and environmental variables, as indicated by RDA (Figure 14), is associated with a biomass-depth gradient. Polychaete biomass shows the strongest relation to the biological data along that gradient, particularly to sample points located away from the origin (e.g. samples 19, 28 and 1526). Samples dominated by macrophages tend to have a higher biomass than those dominated by microphages (e.g. samples 6 and 94). Assemblages which show a predominance of microphagous polychaetes tend to be located in habitats with strong current regimes. Off Labrador, these are usually found in deep water, away from the 200m isobath, where predicted average temperatures are higher than in shallow water (see Appendix D).

The proportion of variance accounted for by the environmental variables in RDA represents 56.1% of the total variation in the biological (percentage) data (Table 5). The remaining variation (43.9%) cannot be explained by the environmental variables (Figure 15).

3.2.2. Feeding microhabitat approach

Abundance data

The primary gradient extracted by MDS (Figure 16) and PCA (Figure 17) in the approach based on microhabitat abundance data corresponds to the total abundance gradient. As in the previous approach, this gradient is represented diagonally in MDS and along the first axis in PCA. A second gradient, perpendicular to the first one in PCA (Figure 17), is associated with the predominance of sediment surface and subsurface feeders at one end of the gradient and water-column and water-sediment surface feeders at the other end. This gradient is not really recognizable in MDS (Figure 16). The differences between the two ordinations are mostly due to sample points which appear at the extremities of the second gradient in MDS (i.e. sample points 5, 6, 41, 90, and 1526) but are located close to the origin (relative to the other sample points) in PCA (Figure 17).

The relationship between the biological and environmental data along the total abundance gradient (Axis 1 in Figure 18) indicates an association with a biomass-depth gradient identical to the one described previously for the approach based on feeding types. The proportion of variance explained by this gradient (44.9% when constrained by the environmental variables) represents about 80% of the variance accounted for by all constrained axes (Table 4). There is, however, 44.2% of the total variance in the abundance data that remains unaccounted for by the environmental variables over all four RDA axes (Figure 19).

Percentage data

The MDS ordination of standardized microhabitat data displays a diagonal gradient which coincides with three UPGMA groupings (Figure 20). It can be

visualized by joining sample points 3 and 94 by a straight line. This gradient is also recovered in the PCA ordination (Figure 21). The latter, however, displays another gradient along Axis 2. The first gradient (Axis 1) is the result of differences in proportion between sediment surface, subsurface and water-column feeders (Figure 21). The second gradient distinguishes samples dominated by water-column and water-sediment surface feeders from those dominated by surface and subsurface feeders. While neither gradient represents exactly the second gradient extracted by PCA with abundance data (Figures 17 and 18), the latter appears to be a combination of the two gradients shown in Figure 21.

Variation among samples in the proportion of individuals per feeding microhabitat along the two gradients (Figure 21) appears to be associated particularly with environmental variables such as current regime, predicted average temperature, depth and sediment granulometry. Out of 15 sample points located in the upper quadrants of Figure 22, 14 represent sites situated at depths less than 200m, on banks and on the edge of banks and of the Marginal Trough (Figure 1). These sites, dominated by water-surface feeders, are mostly characterized by sandy bottoms (as indicated by SILT, CLAY and GRAVEL arrows pointing away from these sample points) and weak current regimes.

Sample points located below Axis 1 (Figure 22) represent sites mostly from deeper areas (15 out of 21), on the upper continental slope, in the saddles or in the Marginal Trough. These sites show a dominance of surface feeders or subsurface and water-column feeders, depending on the position of the sample point relative to Axis 1. Sample points located in the lower left quadrant of Figure 22 represent sites which show a dominance of surface feeders and are associated with high biomasses and fine sediments. On the other hand, sample

points to the right of Axis 2 represent sites with a dominance of subsurface and water column feeders. Many of these sites are characterized by coarse sediments (see Figure 4) and/or are found in the northern part of the study area, at great distances from the shoreline.

Environmental variables explained only 35.3% of the total variation in the biological (percentage) data (Figure 23). This proportion (i.e. sum of eigenvalues for all constrained axes) as well as the proportion of variance explained by the first axis alone is not statistically significant (Table 5). Therefore, results from the biological-environmental biplot (Figure 22) must be interpreted with caution.

3.2.3. Motility pattern approach

Abundance data

In this approach based on the absolute frequency of polychaetes among motility patterns, the primary gradient extracted by MDS (on a diagonal; Figure 24), UPGMA (Figure 24) and PCA (Figure 25) corresponds again to variations in total polychaete abundance among samples. All analytical methods also distinguished a second gradient. This gradient separates samples dominated by sessile-discretely motile polychaetes from samples dominated by polychaetes exhibiting one of the other three motility patterns (Figure 25).

The relationship between the total abundance gradient and environmental variables (Axis 1; Figure 26) is identical to the one described for the previous approaches. Along the second axis, the relationship between the biological and environmental data is not strongly associated with water depth. Samples dominated by sessile-discretely motile polychaetes tend to be from sandy bottoms, in areas of weak current regimes. Samples which show a predominance of sessile polychaetes tend to be from sites with strong current regimes, high predicted average temperature (3-4°C) and fine sediments, particularly clay (Figure 26).

The proportion of variance accounted for by the environmentally constrained axes represents about 60% of the total variance (Table 4). The remaining variance (Figure 27) cannot be explained by the environmental variables used in this study.

Percentage data

Results of MDS/UPGMA (Figure 28) and PCA (Figure 29) are comparable to each other and do not display any strong gradient; most sample points are located in a more or less tight circular cloud as opposed to a linear arrangement (e.g. Figures 24 and 25). However, four out of five deep-water samples from the vicinity of Hudson Strait are separated from the rest of the samples. These four samples show very low total abundance (Figure 25), but tend to be dominated by sessile polychaetes (samples 4, 5 and 6) or by sessile and discretely motile polychaetes (sample 3; Figure 29). The remaining samples are distinguished mostly on the basis of differences in proportions of sessile, discretely motile and motile polychaetes (Figure 29).

The relationship between the PCA (samples/motility patterns) ordination and the environmental variables is shown in the RDA biplot (Figure 30). Samples dominated by motile polychaetes (lower left quadrant of Figure 30) tend to come from shallow-water sites where biomasses are usually high and sediments are mostly sandy. Samples with a predominance of sessile, and to a lesser degree of discretely motile polychaetes (right side of Figure 30), tend to be associated with deep-water sites with strong current regimes and high predicted average temperature (3-4°C). These sites are also characterized by a tendency to have high clay content in the sediment, with occurrence of gravel in some cases. Samples with high proportions of discretely motile polychaetes (upper left quadrant in Figure 30) usually come from sites which show a mixture of

environmental conditions. In other words, there does not seem to be any tendency among sites to be associated with linear gradient such as water depth, biomass or clay content. At best, these sites tend to be located at great distances from the 2000m isobath (i.e. nearshore) and/or from the 200m isobath (e.g. on the banks).

The proportion of variance explained by the environmental variables on all constrained axes represents 66.4% of the total variance in the standardized data (Table 5); 47.6% of the total variance is accounted for by the first axis alone. The remaining variance (33.6%) cannot be explained by the environmental data (Figure 31).

3.2.4. Body size approach

Abundance data

The total abundance gradient described for the previous functional approaches is also recovered by the three analytical methods applied to the body size (abundance) data (Figures 32 and 33). Variation along a second gradient (Axis 2 in Figure 33) appears to be mostly associated with the predominance of small or large polychaetes in the samples. Samples with a predominance of large individuals (ESD > 2.0mm) tend to be found at shallow-water sites where sediments are mostly sandy and biomasses are high (Figure 34). On the other hand, samples with predominantly small individuals tend to be from deep-water sites, often with strong current regimes (lower right quadrant in Figure 34), or from sites away from the 2000m isobath, mostly in the southern part of the study area (lower left quadrant in Figure 34).

The proportion of variance explained by all constrained axes (58.7%) is similar to that of the previous approaches (Table 4 and Figure 35). However, the first axis alone explains less variation (41.2%) in comparison to the previous

approaches. Since the first axis always represents the total abundance gradient, the proportion of variance explained by this axis tends to vary directly with the total variance for each data set (i.e. with the number of biological variables in each approach). This is particularly obvious when comparing the eigenvalues for Axis 1 among approaches for PCA alone (Table 4).

Percentage data

Ordinations of body size data from MDS and PCA show very similar patterns (Figures 36 and 37). Three major groups of samples (i.e. two gradients) can be distinguished from these ordinations and from UPGMA groupings (Figure 36). Samples to the right of Axis 2 (Figure 37) are characterized by a dominance (in proportion) of small polychaetes while those to the left show a predominance of larger individuals. Sample points in the upper left quadrant represent sites where polychaetes are largest on average (i.e. predominance of individuals with 4.0mm $\leq$ ESD $<$ 8.0mm).

The relationship between these patterns and environmental variables is shown in Figure 38. In this case the RDA ordination of biological (percentage) data is a mirror image of the PCA ordination (Figure 37). This only represents an arbitrary change in the orientation of Axis 1. Samples dominated by the largest individuals tend to be associated with high biomasses. Several of these samples come from sandy or sandy-muddy sites (Figure 4) at various depths. The two other groups of samples are primarily associated with a depth gradient. Samples with a predominance of medium-sized polychaetes (1.0mm $\leq$ ESD $<$ 4.0mm; Figure 38) tend to be from deep-water sites (9 out of 12 samples from depths $>$ 200m), where current regimes are strong and predicted average temperatures are high. Several of these sites are located in the northern part of the study area, at great distances from the shore line. Finally, samples with high

proportions of small polychaetes (ESD < 1.0mm) are mostly from shallow-water sites (11 out of 16 samples, from depths < 200m; see Figure 1), frequently located nearshore, as indicated by the positive correlation with distance from the 2000m isobath and negative correlation with distance from shore (Figure 38).

The proportion of variance in the percentage data explained by the first constrained axis is low (35.1%) but significant (Table 5). It represents slightly more than half of the variance explained by all constrained axes. Overall, 33.8% of the total variance is unaccounted for by the environmental data (Figure 39).

3.2.5. Foraging mode/body size approach

Abundance data

In this approach, the three analytical methods show some separation of sample points along the total abundance gradient (Figures 40 and 41). In the MDS ordination, this gradient runs diagonally from the lower left corner to the upper right corner of Figure 40. About 25 of the 36 samples, however, appear in a tight cluster at one end of this gradient (Figure 40). Samples with low total polychaete abundances (i.e. less than 35 individuals; see Table E-1) are separated from the bulk of the samples. The PCA ordination shows a more even spread of sample points over the full gradient (Axis 1; Figure 41).

The configuration of sample points in MDS along the second gradient (i.e. perpendicular to the first gradient; Figure 40) resembles that of the PCA along the same gradient and distinguishes samples on the basis of proportions of the different foraging mode/body size categories (Figure 41). UPGMA does not display a second gradient. The relationship between the total abundance gradient and environmental variables (Figure 42) is identical to the one described previously for the other functional approaches. A detailed description of the second and following gradients, which are related to proportions of

individuals among functional categories, and their relationship to the environmental variables is presented in the following section.

About 24% of the variance in the abundance data is accounted for by the first constrained axis, which represents almost half of the variance explained by all constrained axes (Table 4). After all constrained axes have been extracted by RDA, half of the total variation remains unaccounted for by axis-environment relationships. When only the first four axes are considered, however, the difference between the amount of variance explained by the environmental data and that explained by unconstrained axes (in PCA) only amounts to about 25% (Figure 43).

Percentage data

The MDS ordination of samples show a gradient that runs parallel to Axis 2 (Figure 44) and which corresponds to the gradient extracted by PCA along Axis 1 (Figure 45). As observed in the previous analysis based on abundance data, PCA tends to spread sample points more evenly along the gradient than MDS. Results of UPGMA are inconclusive since it produces essentially only one cluster of sample points. PCA also extracts a second gradient along Axis 2 (Figure 45) which is not represented in the MDS ordination (Figure 44).

While there is no evidence of well-defined clusters of sample points based on the analysis of percentage data, most points are distributed along two gradients (Figure 45). These gradients are also represented on the RDA biplot (Figure 46), although as a mirror image of the PCA ordination (Figure 45). The primary gradient can be visualized by drawing a straight line between sample points 4 (lower left quadrant of Figure 46) and 1526 (upper right quadrant). Another set of sample points situated in the upper left quadrant (Figure 46) defines the second gradient.

Four groups of samples can be distinguished on the basis of their position along the two gradients in the ordination diagram. In the first group, located in the upper left quadrant of Figure 46, 4 out of 7 sample points represent sites on the eastern edge of the Labrador Banks (Figure 1). These sites are dominated by large, motile macrophagous polychaetes and are associated with high biomasses and relatively low occurrence of gravel on sandy sediments (Figure 46).

The remaining sample points distributed along the first gradient represent sites located on banks, in the saddles (i.e. between banks) and in the Marginal Trough. Of the nine sample points found toward the extreme left of the lower left quadrant in Figure 46, eight points correspond to sites between banks, at depths greater than 200m. At these sites, current regimes are strong, sediments are coarse and polychaete assemblages tend to be dominated by medium-sized sessile microphages.

The third group is represented by 13 sample points located in the extreme right portion of Figure 46. Nine of these sample points correspond to sites on banks or nearshore (i.e. west of the Marginal Trough), usually at depths less than 200m. The three samples from Hermitage Channel are also included in this group, even though the depth exceeds 300m (Table 1 and Figure 1). These sites are characterized by a dominance of small motile and discretely motile macrophages and microphages (Figure 46) and are located mostly in shallow-water habitats where fine sediments and weak current regimes occur.

Sample points situated at or near the origin of the biplot (i.e. samples that cannot be distinguished by Axes 1 and 2 in Figure 46) from the fourth group. Five out of seven sample points in this group represent sites in or near the Marginal Trough. These sites display a mixture of all functional categories and are probably exposed to a mixture of environmental conditions.

The relationship between Axis 1 and the environmental variables, although significant, explains only 14.7 % of the total variation in the percentage data (Table 5). After all constrained axes have been extracted, nearly 50% of the total variance is explained, leaving the other half of the variance unaccounted for by the environmental variables (Figure 47).

3.2.6. Taxonomic approach

Abundance data

The analysis of family abundance data by MDS shows a gradient from the lower left corner to the upper right corner of Figure 48, which generally corresponds to the total abundance gradient observed in the PCA ordination (Figure 49) and in the previous approaches. There are, however, some sample points which do not follow that gradient (e.g. samples points 30, 11 and 90; Figure 48). Results from UPGMA are inconclusive (Figure 48).

The relationship between the biological and environmental data along the total abundance gradient (Axis 1; Figure 50) follows the pattern described previously for the other approaches, with 20% of the total variance explained by the first constrained axis (Table 4). About half the variation in the abundance data is accounted for by all constrained axes Figure 51). Details of patterns and relationships associated with differences in proportion among families (Axis 2 and following) are examined in the following section.

Percentage data

The MDS ordination of samples based on polychaete family (percentage) data shows a diagonal gradient (upper left corner to lower right corner of Figure 52) which is similar to the one represented by Axis 2 of the PCA ordination (Figure 53). UPGMA groupings also follow this gradient. The PCA ordination shows, however, a gradient along Axis 1 (Figure 53) which is not represented in the MDS ordination (Figure 52).

The two gradients displayed in Figure 53 are mostly associated with samples dominated either by Cirratulidae (lower left quadrant in Figure 53), by Sabellidae, Nephtyidae and Spionidae (upper left quadrant in Figure 53), or by Maldanidae and Onuphidae (right side of Figure 53). This pattern, however, is modified when environmental constraints are imposed by RDA (Figure 54). Samples with a predominance of onuphid polychaetes are separated from those which are characterized by a predominance of maldanids, particularly sample 4 and to a lesser extent sample 24. Samples dominated by cirratulids are brought closer to those dominated by nepthyids and spionids. Finally, samples with large proportions of sabellids are associated with samples dominated with terebellids (Figure 54). The resulting sample ordination shows patterns which are very similar to those displayed by the RDA sample ordination based on the foraging mode/body size approach (Figure 46). The primary gradient can be visualized by a straight line joining sample points 5 (or just above) and 90 (Figure 54). Sample points in the upper quadrants of Figure 54 are distributed along the second gradient, perpendicular to the first one.

Overall, sample points located close to each other in Figure 54 are usually found close to each other in the RDA biplot based on the foraging mode/body size approach (Figure 46). In fact, with the exception of some minor shift in the location of sample points relative to each other, the most important difference between the two biplots is the orientation of the gradients in relation to Axes 1 and 2; the taxonomy-based biplot displays a rotation of about 45 degrees. This feature of the biplots does not affect the interpretation of the relationships between the biological and environmental variables. Another difference between the two approaches is the fact that sample points along the first gradient in the foraging mode/body size-based biplot (Figure 46) show a better separation than

those in the taxonomy-based biplot (Figure 54). In the latter, the points are aligned in a narrower band along Axis 1 (i.e. smaller range on Axis 2).

Four groups of samples can be distinguished in the taxonomic approach based on percentage data. These are very similar to those described for the foraging approach (Figure 46). The first group includes sample points situated in the upper quadrants of Figure 54. These represent for the most part (4 out of 7 samples) sites on the eastern edge of banks. The large motile macrophages which dominate the polychaete fauna at these sites are mostly members of the family Onuphidae (Figure 54). As in the previous approach (Figure 46), this group of samples shows a strong association with areas of high biomasses and sandy bottoms, usually near the 200m isobath.

In the second group, represented by seven sample points situated at the extreme left of the lower left quadrant and by sample point 4 in Figure 54, seven out of eight points correspond to sites between banks (i.e. saddles) and deeper than 200m. These sites are particularly dominated by Maldanidae, Terebellidae and Sabellidae. Of the thirteen sample points situated in the lower right quadrant (extreme right) of Figure 54 which form the third group, nine points represent sites on banks or nearshore (depth < 200m). At these sites, polychaete assemblages are dominated by Nephtyidae, Cirratulidae and Spionidae. In the fourth group of sample points, located near (sample point 1) and below the origin (Figure 54), five out of eight points represent sites in or near the Marginal Trough. Samples from this group contain a mixture of all families.

The relationship between these groups (or patterns) and the environmental variables along the primary gradient is very similar to the one described in the foraging mode/body size approach. In the taxonomic approach,however, it appears that the relationship is more complex, as indicated by the fact that

many arrows (i.e. environmental variables) are not oriented along the gradient as in Figure 46 but rather in various directions (Figure 54). This indicates that several environmental variables are contributing to the separation of samples along both gradients. Monte Carlo tests indicate that the relationship between the first eigenvalue (Axis 1) and the environmental variables is significant ($p < 0.01$) while the relationship between the sum of all eigenvalues (i.e. trace) and the environmental variables is not significant ($p = 0.14$). The amount of variation explained by each axis (Figure 55) is very similar to the one obtained by the foraging mode/body size approach (Table 5).

Note added after the oral defense

Dr. Richard Warwick, the external reviewer, reports that his colleage Dr. K. R. Clarke has recently developed a program called BIOENV which attempts to correlate multivariate faunistic patterns with ordinations of environmental variables. It essentially compares the rank order of dissimilarities in the dissimilarity matrix underlying the MDS with the rank order of dissimilarities underlying an environmental variables PCA (i.e. euclidean distances). The measure of rank correlation between these matrices weights the lower ranks more heavily than the higher ranks in order to match adequately the fine structure of the ordinations.

Warwick applied this method to $\sqrt{\sqrt{}}$-transformed abundance data for the foraging mode/body size appproach (Appendix Table E- 3) and the taxonomic approach (Appendix Table E-4), using the Bray-Curtis similarity measure and all sixteen (untransformed) environmental variables (Appendix Tacle C-2). The correlation found for the taxonomic approach ($r= 0.441$) was greater than for the functional approach ($r= 0.371$). These correlation were raised to 0.491 (taxonomic) and 0.427 (functional) when environmental variables POLYWT, TOTALWT and the four sediment grain size variables were root-transformed.

The validity of BIOENV has not been examined critically through publication. Also, it appears that the environmental variables may not have been standardized prior to the PCA. This would result in weighing variables with a wide absolute range of values more heavily (e.g. NEWLAT, DEPTH, distances). Finally, with this method a maximum of 24% of the variance in the taxonomic (dissimilarity) matrix is explained by the correlation with the environmental PCA matrix. In the thesis, the method used which has been published in peer-review journals accounts for more than 50% of the variation in the biological data with fewer environmental variables.

J.-M.G.

4. DISCUSSION

4.1. Comparison of functional and taxonomic approaches

The ability of marine benthic animals to establish and maintain themselves under certain environmental conditions is mostly determined by physiological requirements, one of which is food intake. In soft-bottom communities, food gathering strategies (foraging patterns) are strongly influenced by environmental factors such as near-bottom currents and sedimentary processes (e.g. Rhoads 1974; Biernbaum 1979; Whitlatch 1981; Jumars and Nowell 1984) and consequently, so are the distribution and abundance of trophic groups among communities. As suggested by the size-dependent structure of benthic communities (Schwinghamer 1981; Warwick 1984; Gerlach *et al.* 1985), body size also plays an important role in trophic relations between organisms and in their distribution and abundance in the benthos. The distribution of sizes in the benthos is influenced by factors such as sediment granulometry and porosity (Schwinghamer 1985).

The functional and taxonomic approaches used in this study have allowed the determination of patterns which can be related to the structure of soft-bottom polychaete assemblages. Here, it is assumed that the observed statistical relationships between the biological and environmental variables are evidence of *in situ* interactions with the environment which influence community structure (Green and Vascotto 1978). It is also assumed that generalities regarding relationships between the distribution and abundance functional categories and the environment for the polychaetes also apply to the other macrofaunal groups within the benthic communities.

Within each approach, recurrent patterns were observed between the different numerical methods, suggesting that these patterns are real and not

mathematical artifacts (Field *et al.* 1982). Therefore, unless indicated otherwise, results from Redundancy Analysis will be used to characterize the structure of polychaete assemblages.

The comparison of the six approaches and their success in providing a strong and meaningful ecological characterization of the community structure, however, is hampered in part by the fact that several of these approaches are based on a different number of biological variables. Consequently, in an approach such as the microhabitat approach, all variability in the biological data can be explained efficiently in a maximum of three unconstrained axes, with most of it explained in the first two axes (see Tables 4 and 5). In contrast, data in the taxonomic approach can be summarized with up to 35 axes, resulting in a greater spread of the variance explained over many of these axes.

This problem is clearly illustrated by the direct relationship between the number of variables in the analysis of abundance data, the total sum of squares (a measure of total variability) and the proportion of variance explained by Axis 1 (Table 4). For instance, while the pattern extracted by the first PCA axis remains the same for all approaches (i.e. total abundance gradient), the variance associated with this pattern represents a proportionally smaller portion of the total variance in approaches with large number of variables than those with small number of variables. In view of this limitation, the practical value of the various approaches will be assessed by determining which approach yields the most meaningful ecological patterns.

One way of qualitatively assessing the ecological value of the patterns is to examine the degree of homogeneity of the different groups of samples being displayed. Strong ecological patterns should be characterized by groups of samples from sites subjected to similar environmental conditions. As indicated

previously, this qualitative assessment can be combined with values of variance explained to determine the most effective approach.

The total abundance gradient extracted by all approaches represents the primary source of variation in the abundance data. This gradient is mostly associated with nutrient availability in marine soft-bottoms. Continental shelves are areas where most of the ocean's primary production occurs, therefore supporting high biomasses and abundance of benthic organisms (Parsons *et al.* 1984). Bathyal water, on the other hand, shows a decreasing benthic biomass and abundance with increasing depth and decreasing food availability (Thiel 1975; Parsons *et al.* 1984).

In addition to supporting this well-documented relationship between benthic biomass and water depth, the total abundance gradient also indicates that benthic communities in southern areas (i.e. samples from the southern part of the sampling range) may be more productive. This observation appears to support the idea that pelagic food particles from subarctic waters are transported to the south by the dominant currents and eventually settle towards the bottom (B. Hargrave, personal communication). nother explanation could be, however, that the shorter growing season in the nothern part of the study area results in lower benthic biomasses and productivity than are found in the southern part. Since, in all six approaches, about 62-64% of the variance associated with the total abundance gradient is explained by the environmental variables used in this study (see Table 4), other factors, biotic or abiotic, probably account for some of the remaining variability. These unaccounted factors will be discussed later in a separate section.

The following gradients extracted by the different approaches represent patterns of variability in the proportions among biological variables. By using

separate functional approaches for each foraging attribute and body size, it is shown that a biological attribute such as feeding microhabitat may not be ecologically important (i.e. do not play a determining role in the structuring of communities), at least as far as it can be assessed from the relationship between the biological and environmental data described in this study. Approaches based on the other functional attributes and taxonomy have extracted patterns which are significantly correlated with the environmental variables (Table 5). Therefore, my first prediction, which sated that a significant statistical relationship exists between the biological and environmental data in a functional approach based on body size and/or foraging attributes, is supported.

Although the feeding type approach would seem to be the most efficient in statistical terms, explaining a large proportion of variance over a very limited number of axes (i.e. 56.1% with one axis), the fact that this approach is based on only two variables limits the number of distinct groups of samples that can be recognized. Samples dominated by macrophagous polychaetes are mostly from sites showing high biomasses while those dominated with microphagous polychaetes (i.e. most samples) have low biomasses. Most samples, however, are not well separated along this gradient, nor by any strong depth-current gradient. This is explained by the dominance of microphages (deposit-feeders) in most habitats (Gaston 1987).

As the number of variables in the approach increases, more groups of samples are distinguished along gradients. Faunal predominance in the samples tends to be associated with environmental conditions more or less typical of large-scale topographic features of the Labrador shelf and upper slope. Shallow areas on banks and nearshore support high biomasses and tend to be dominated by motile polychaetes (Figure 30). Deep-water sites (i.e. saddles, Marginal

Trough and slope), on the other hand, are exposed to stronger current regimes and show a predominance of sessile polychaetes. Samples with a predominance of discretely motile polychaetes tend to be found at various depths, under a mixture of environmental conditions.

The dominance of body size classes among samples shows a somewhat different pattern, indicating that approaches based on motility pattern and body size do not provide redundant information on the community structure. Large individuals tend to predominate polychaete assemblages in areas of high benthic biomass from various depths. Shallow-water areas show a predominance of small polychaetes while in deep water, particularly in the northern part of the sampling range, medium-sized individuals dominate.

The combination of all functional attributes in one approach (i.e. foraging mode/body size approach) seems to provide the best characterization of the biological data (second prediction). The patterns extracted by unconstrained PCA (Figure 45) are in good part associated with large-scale topographic features of the study area. (i.e. banks and nearshore, eastern edge of banks, saddles, and Marginal Trough). This is supported by the environmental gradients from Redundancy Analysis (Figure 46) which describe environmental conditions associated with these topographic regions.

Distinct functional categories dominate polychaete assemblages within these regions. These categories, however, do not always compare with those observed in other studies under similar environmental conditions (e.g. Fauchald and Jumars 1979; Massad and Brunel 1979; Maurer and Leathem 1981; Gaston 1987). Sessile polychaetes, for instance, usually dominate soft-bottom assemblages under physically stable conditions (i.e. weak currents and fine sediments; Gaston 1987). The present study relates their predominance to

physically unstable habitats (i.e. saddles) where current regimes are strong to moderate and sediments tend to be coarse (see Figure 46). A possible explanation for this discrepancy is the fact that habitats in saddles (including vicinity of Hudson Strait) may not be comparable to any of the soft bottoms considered by the other studies. The occurrence of coarse sediments, with a fair proportion of gravel (i.e. particle size greater than 2mm; see Appendix C), indicates that this habitat may resemble hard bottoms more closely, where physical stress and rate of disturbance are high (Sousa 1984; Menge and Sutherland 1987). Tube-building polychaetes attached to rocks, albeit not quantified, were frequent at the sites.

Another reason for this difference may be related to sediment dynamics. Because sediments at these sites also contain large proportions of mud, it is possible that larger particles (i.e. pebbles, cobbles and rocks) serve to stabilize the soft bottom and reduce sediment erosion by altering near-bottom currents. This would make that particular habitat suitable for sessile (tube-building) polychaetes. Large quantities of unattached worm tubes (mostly maldanids) found at these sites support the latter explanation.

In other studies, macrophagous polychaetes have been shown to dominate in shallow soft-bottom assemblages where sediments are coarse and less stable, due primarily to greater physical disturbance by currents and wave actions. It has been hypothesized that this preference of macrophages for coarse sediments is related to the pore space between sand grains. Greater pore space allows movement of macrophages and increased oxygen penetration in the sediment (Maurer and Leathem 1981; Gaston 1987). Results from the present study, however, show a different pattern in the predominance of macrophages. Large macrophages were observed at relatively deep-water sites (i.e. eastern edge of

banks) and did not appear to be otherwise correlated with depth or current regime. Sediments were mostly sandy and supported high benthic biomasses.

This result differs from that of previous studies probably because of the predominance of a single species, the onuphid worm *Nothria conchylega* (see Figure 54). This species has been considered as a carnivore (i.e. macrophage) in the present study and by Maurer and Leathem (1981), while Gaston (1987) considered it as a deposit-feeder (i.e. microphage). Like several onuphid species the feeding habit of *Nothria conchylega* is probably better described as omnivore (Fauchald and Jumars 1979). Under this redefinition of the feeding type, onuphids may alternate between macrophagy and microphagy, depending on environmental conditions prevailing at the time (e.g. food availability) and/or changes in feeding preference during their life cycle. Their association with sandy sediments, high benthic biomasses and outer shelf edge (i.e. where high planktonic productivity and large amounts of detritus occur) supports previous observations for surface-deposit (microphage) feeders (Gaston 1987).

Small motile macrophages and discretely motile microphages share the dominance in shallow habitats (i.e. water depth less than 200m on banks and nearshore; see Figure 46). At these sites, current regimes are usually weak (Fissel and Lemon 1982) and sediments are made up of a large proportion of silt and little, if any gravel. In this study, the predominance of these two functional categories appears to decrease with water depth while Maurer and Leathem (1981) have observed the inverse. Jumars and Fauchald (1977) also found a relationship between water depth and the ratio of sessile to discretely motile polychaetes. This relationship is influenced by sediment stability and flux of organic matter. On the Labrador shelf and upper slope, sediment stability, and not depth, may be the environmental factor affecting the distribution and abundance of discretely motile polychaetes.

The predominance of small, motile macrophages on banks and in the nearshore, however, does not follow patterns observed in previous studies. This habitat, although in relatively shallow water (i.e. less than 200m), tends to have finer and potentially more stable sediments, as suggested from weak current regimes, than habitats where macrophages usually dominate (Gaston 1987). The vast majority of small macrophages observed on the Labrador shelf belong to the family Nephtyidae. *Aglaophamus malmgreni* is the most common nephtyid polychaete in that size range found in the Labrador region (Pocklington and Tremblay 1987). Although no data is available on the feeding of this species, it is assumed that, like most nephtyids, it is primarily carnivorous. Reports of detritus feeding, however, are available for some nephtyid species (Sanders 1960; Fauchald and Jumars 1979).

The discrepancy between the patterns of macrophage dominance in this study and other studies can probably be explained by one of two reasons: 1) previously described patterns do not apply to the geographic area under study, or 2) *A. malmgreni* is not restricted to carnivory (macrophagy) but can also feed on deposited detritus. While these remain to be tested, the small size of *A. malmgreni* (i.e. average total body length < 10mm; see Appendix B, Figure B-21)) would support the latter reason.

In this study, the taxonomic approach was based on a classification of polychaetes at the family level. Heip *et al.* (1988), Warwick (1988) and Ferraro and Cole (1990) have demonstrated that multivariate analyses based on family data, when compared with analyses based on species data, show no loss of information and often provide a better separation of samples. Furthermore, when comparing results from eigenvector ordination analyses, the amount of variation explained in the data is greatly dependent on the initial number of

biological variables entered in the analysis (see above). By using a taxonomic classification to family, the resulting number of variables is comparable to the number of functional categories, thus allowing a direct comparison of two approaches in terms of proportion of variance explained. Because of the dominance of few single species (see below), ordinations based on species data tend to be similar to those based on family data.

The taxonomic approach yielded results similar to the foraging mode/body size approach, in patterns displayed in the biplot diagrams as well as in the amount of variation explained. These similarities in the results of two approaches which, in principle show little overlap in the biological categories (variables), can probably be explained by the strong dominance of a limited number of taxa in the study area. For instance, *Nothria conchylega* was the only representative of the family Onuphidae and dominated polychaete assemblages in at least five samples (see Appendix E, Table E-4). Individuals of this species also accounted for the bulk of the large-sized motile macrophages examined in this study. Similarly, *Aglaophamus malmgreni* accounted for most specimens in the family Nephtyidae and in the small-sized macrophage categories. The other dominant polychaete families (e.g. Cirratulidae, Maldanidae, Sabellidae, Spionidae and Terebellidae; Figure 54) were usually represented by more than one species but these species were often assigned to one or few functional categories. The result is that the same dominant groups influenced the outcome of multivariate analyses in both approaches.

Results from the functional approach based on foraging mode and body size, however, appear to be better than the taxonomic approach, as indicated by a better separation of sample points in the ordinations, particularly along the depth gradient (third prediction). Furthermore, without insights from the

functional approaches on the trophic structure of polychaete assemblages, results from the taxonomic approach would not be easily interpreted in terms of interactions with the environment. This supports the idea that the functional approach is appropriate to study processes underlying the structure of these benthic communities. On the other hand, the classification of samples from Hermitage Channel (305-375 m) with those from shallow areas of the Labrador shelf (< 200 m) suggests that observed patterns associated with large topographic features may not apply to other geographic areas. In fact, as indicated earlier, compositional patterns observed in the present study for the polychaete foraging attributes are not completely comparable to those from other geographic areas.

Some improvement in the proportion of variance explained by the canonical analysis can be obtained by reducing the number of variables, especially those that did not contribute significantly to the biological patterns. This can be achieved in the functional approach based on foraging mode and body size by omitting information on feeding microhabitat since the approach based on the latter attribute did not produce patterns that were significantly correlated with any of the environmental variables. The resulting approach contains fewer biological variables (i.e. 24 functional categories; see Figure 2) and, as indicated from Redundancy Analysis, shows patterns comparable to the foraging mode/body size approach (Figure 46). The variance explained by the axis-environment relationship now represents 59.3% of the the total biological variance; 51.3% of the total variance is explained by the first four constrained axes alone, compared with 38.9 % for the foraging mode/body size approach. This increase in the proportion of variance explained, albeit substantial (i.e. about 32% over the first four axes, and 15% over all axes), could not be tested for

statistical significance. Still, any approach which does not compromise on the ecological information by reducing the number of descriptors (i.e. extract the same patterns from the biological data as a more comprehensive or standard approach) while explaining as much, if not more, biological variability should be considered as a valuable alternative approach. This is essentially the advantage of the taxonomic approach based on families.

4.2. Importance of environment in community structure

Using the various functional approaches based on foraging attributes and/or body size and the taxonomic approach, this study shows that environmental conditions associated with large-scale topographic features of the Labrador continental shelf and upper slope contribute substantially to processes underlying the structure of benthic polychaete assemblages. The lack of discrete clusters of samples in the ordination biplots (Figure 3) strictly associated with large-scale topographic features and the fact that only half of the total biological variance was accounted for by the environmental variables used in this study suggest, however, that other process are probably involved. The remaining variation not accounted for in the analyses may either be associated with undetermined processes (i.e. not correlated with our environmental variables) or may simply be noise (Gauch 1982b; ter Braak 1986). Factors such as stability, water and organic content, O_2 content and microbial biomass of sediment have been shown to be significantly correlated with the trophic composition of soft-bottom communities (Maurer and Leathem 1981; Gaston 1987). Quantitative estimations of these factors were not available for this study. Substrate disturbance due to iceberg scouring is ubiquitous on the Labrador shelf (Lewis *et al.* in press). The effect of scouring on community structure and the time since the last disturbance may be important (Woodin 1978) but cannot be evaluated from this study.

Several biotic factors can also affect the structure of benthic communities (Wildish 1977; Parsons *et al.* 1984). Woodin (1974) showed by cage experiments that competitive interactions and behavioural patterns can determine the abundance patterns of soft-bottom polychaetes. Similarly, selective predation based on size and susceptibility (microhabitat considerations), for instance, can probably alter the relative abundance of benthic animals and consequently, the community structure. Activities in the sediment by deposit feeders have been shown to lead to the exclusion of suspension feeders (Rhoads and Young 1970). Adult-larvae interactions, larval settlement success and larval predation can also affect community structure (see a brief review in Parsons *et al.* 1984). These and other biotic factors may account for some of the variability in the biological data that remains unexplained by the environmental data used in this study.

A closer examination of the proportion of variance explained by each axis, however, tends to indicate that it is unlikely that any single biotic or abiotic variable will account for the remaining 48-49% of the variation in the biological data. When considering only the first four axes, a difference of 21-28% exists between the variation accounted for by constrained and unconstrained axes. At best, an 'ideal' variable would explain an equivalent amount. The remaining variation in the 5^{th} and following axes is assumed to be largely noise (Gauch 1982b). In reality, most biological and environmental factors are correlated to each other to some extent, as is the case for variables used in this study. Therefore, the amount of variation accounted for by a new variable such as sediment water content would probably be less than 20%. This does not preclude water content from influencing the outcome of the analysis or its interpretation. It is reasonable to assume that water content would be included along with the other interacting variables in a complex environmental gradient similar to that observed in Figure 46.

4.3. Effect of sampling scales

Some environmental variables used in the analysis (e.g. temperature, current regime) incorporate large temporal and spatial scales that may not always provide a good estimation of the conditions to which endo- and epibenthic organisms are exposed during their relatively short lifespans. Small-scale processes such as near-bottom fluid and sediment dynamics, on the other hand, affect settling and foraging patterns of these organisms (Jumars and Nowell 1984) but are not easily quantifiable during large-scale sampling surveys. Some of the small and medium scale processes are the result of biological activities within the sediment (e.g. bioturbation, sediment consolidation; Rhoads and Young 1970; Tevesz and McCall 1983). Most likely, the observed patterns in faunal composition over the Labrador shelf and upper slope are the result of processes acting at spatial scales ranging from a geographic area (e.g. Labrador shelf) to the ambit of an individual organism (Dayton and Tegner 1984; Wiens *et al.* 1986).

Better estimations of the biotic and abiotic factors that affect benthic community structure can probably be achieved by determining the temporal and/or spatial scales at which these factors interact with the organisms. This may result in an improved correlational relationship between biological and environmental data in multivariate analyses. The logistics involved in getting such estimations, however, would be phenomenal since the scales at which interactions are most significant tend to vary with body size, life style and life span of each organism in the community. Ultimately, several scales for the same factor may provide insights into different, but still valid ecological processes that affect the community structure (e.g. competition vs. predation; Dayton and Tegner 1984; May 1984; Wiens *et al.* 1986).

In a community approach, it is obvious that one cannot attain such a detailed quantification of the biotic and abiotic factors while adequately sampling the fauna. Improvement of the estimations could still be achieved for some of the environmental variables used in the present study. For instance, sediment data would be ecologically more meaningful if restricted to the top 10cm of sediment where most endobenthic organisms are found, instead of the 'homogenized subsample which averages sediment granulometry over the entire grab sample. Water temperature and current regimes can be refined by adding recent near-bottom data from each sampling site to the existing large-scale information.

4.4. Advantages and disadvantages of a functional approach

A typical problem associated with benthic sampling in ecology is the substantial investment in time and research funding required to obtain and process endobenthic samples. Appreciable amounts of time are usually spent sorting and identifying benthic organisms to species, especially if the faunal taxonomy of the geographic area under investigation is poorly documented. The use of a functional approach based on biological attributes such as foraging mode and body size reduces the taxonomic investment by limiting the classification to higher taxonomic levels. Emphasis is now directed toward ecologically important characteristics of benthic organisms. From a statistical point of view, the limited number of functional categories, compared with the usually large number of species found in a sample, will often result in stronger patterns (i.e. more variability explained by fewer axes). More importantly, groupings of samples from multivariate analyses represent faunal assemblages that can be readily interpreted in terms of interaction among functional groups and between these groups and the environment. The taxonomic approach, when used separately to

study the community structure, still requires a fair investment gathering trophic information on each species. This information is introduced indirectly at the end of the analysis to interpret the results.

Another limitation of a taxonomic approach based on classification to species level is related to the restricted geographic range over which distinct communities can be found. With the exception of a few cosmopolitan species, invertebrate assemblages from the Labrador shelf are different from those found in the eastern Atlantic, even though environmental conditions may be similar. The lack of faunal (taxonomic) similarity between regions limits the comparison of community structure, unless information on feeding ecology is included *a posteriori*. The distribution and abundance of functional categories, on the other hand, tend to be associated with environmental gradients and not with geographic regions (for example, see Sprules and Holtby 1979), therefore providing a better tool to reach generalization on the structure of marine soft-bottom communities.

The assignment of benthic organisms to functional categories does require, however, a minimum amount of taxonomic information. In the present study, polychaetes were used because of their predominance in most marine soft-bottom communities and the availability of data on their feeding ecology. Classification of worms to the family level was usually sufficient to determine the foraging mode (Fauchald and Jumars 1979). Fine-tuning of this functional characterization can also be achieved by stomach analysis (Gaston 1987). This method serves to distinguish between different foraging modes within a family and may parallel the taxonomic classification to lower levels.

Invertebrate groups for which the feeding ecology has not been investigated extensively could be considered in a functional approach by identifying

morphologically distinct groups (i.e. presumptive species) and analysing stomach contents on a subsample of individuals from each group. Variation in feeding with body size should also be considered to represent as accurately as possible the trophic structure of the community. While the time spent determining the actual foraging mode for those distinct groups in a benthic sample may be equivalent to the time required to identify organisms to the species level in a standard taxonomic approach, it is obvious that the trophic information acquired can be more profitable from an ecological point of view. The taxonomic approach based on families certainly requires a smaller investment in classification than the functional approach or the 'species' approach, but it still suffers from the lack of ecological information such as body size and foraging behavior.

As mentioned previously, a disadvantage of the functional approach is the lack of detailed information on feeding for most invertebrate groups found in the marine benthos. Substantial investment would be required to perform stomach analysis, particularly on small specimens such as young macrofaunal or meiofaunal organisms. While the use of feeding information from the literature, when available, can greatly facilitate the classification in functional categories, published generalizations may also result in inaccurate or over-simplified characterizations of communities (Dauer 1984). Also, in a functional approach based on body size, estimation of size for a large number of specimens is most efficient with an image analysing system which may increase the financial investment.

4.5. Predictions

Earlier, predictions were made concerning relationships between the biological data and the environmental variables. The first prediction stated that significant relationships exist in the functional approaches. Only one functional

approach in this study (i.e. feeding microhabitat) did not show any statistically significant relationship. In the other five approaches, including the taxonomic one, biological patterns were significantly correlated with the environmental variables, as shown by the Monte Carlo tests.

As mentioned previously, the comparison of approaches with a different number of biological variables is limited to the qualitative examination of the ecological patterns extracted since the total variability and the amount of variance explained in multivariate analyses is highly dependent on that number. Consequently, the second prediction on the comparison of statistical significance among functional approaches is not strictly testable. The ecological meaning of patterns extracted, however, supports this prediction. The functional approach which includes all or most foraging attributes and body size provides the most meaningful characterization of community structure. Concerning the third prediction, only the latter functional approach shows a better relationship between the biological data and environmental variables than the taxonomic approach, not so much in terms of variance explained but in the ecological patterns extracted by the canonical analysis.

Finally, the present study shows that sediment grain size does contribute significantly to the structuring of endobenthic polychaete assemblages (fourth prediction). It is shown, however, that many of the environmental variables, including sediment granulometry, are correlated to each other to some extent. Nevertheless, variables such as water depth, current regime and benthic biomasses tend to be more strongly correlated with the biological patterns than they are to other environmental variables. The ability of a functional approach to predict benthic community structure from the knowledge of a limited number of environmental variables remains to be investigated by including a greater

variety of habitats and geographic areas. This study suggests that there is at least a 50% chance of predicting the right polychaete assemblage from the knowledge of the same twelve environmental variables used here. In the context of habitat management and disturbance-impact study, this probability may still be inadequate (Dauer 1984, May 1984) and no better than by chance alone.

5. CONCLUSION

This exploratory investigation of marine soft-bottom polychaete assemblages indicates that several biological attributes of marine benthic polychaetes may play an important role in the structuring of their communities. Of particular interest are feeding type, motility pattern and body size which, when united through a functional approach, provide an ecologically meaningful characterization of polychaete assemblages. Improvements were found with this functional characterization (i.e. ordination of samples) as compared with the taxonomic one. The availability of information on potential trophic interactions between functional categories and between these categories and the environment, however, allows for a more direct and efficient way of understanding community structure. This study also suggests that the microhabitat (stratum) in which benthic polychaetes feed may not be one of the biological attributes involved in the structuring of communities.

Biological patterns extracted by multivariate analyses are primarily associated with two environmental gradients: benthic biomass and water depth/current regime. No distinct polychaete assemblages are recognized from the analyses. Instead, there is a gradual shift from one type of faunal association to another along the environmental gradients. Among the environmental factors that follow these gradients, sediment grain size is shown to be significant associated with patterns of community structure. This study shows, however, that community structure is most likely influenced by several environmental factors and not just by one or two. This ecological complexity could explain the lack of discrete faunal assemblages along the gradients. A substantial portion of the unexplained variability, however, is probably due to noise. Therefore, it may not be realistic to try to explain all of the biological variability (Gauch 1982b; Jongman *et al.* 1987).

Evidence from this and other studies on population and community dynamics supports the idea that the observed patterns are ecologically real and not just apparent (i.e. simply statistical properties of the system ; May 1984). The goal of the analyses presented here is to distinguish ecological patterns from noise. Results show that with the functional approach, the ability to predict benthic community structure from the knowledge of important environmental variables will require further tests with more extensive data sets. The assignment of benthic polychaetes to functional categories based on published information has allowed ecologically meaningful characterizations of soft-bottom communities. Fine-tuning of these categories and their assignment, however, is possible (with some investment) and may result in an improved community characterization.

Table 1. Benthic sampling sites on the Labrador continental shelf and slope and in Hermitage Channel.

STATION	LATITUDE	LONGITUDE	DEPTH (M)
1	61°33.84'N	61°59.28'W	594
3	61°08.36'N	63°09.62'W	618
4	60°53.98'N	63°54.96'W	385
5	60°35.15'N	61°28.14'W	438
6	60°23.30'N	62°08.24'W	318
8	60°01.00'N	63°44.28'W	128
10	59°44.80'N	61°31.80'W	183
11	59°30.70'N	62°04.64'W	146
12	59°21.83'N	62°29.68'W	128
15	58°56.40'N	61°42.24'W	155
17	59°06.20'N	61°47.70'W	144
19	58°36.70'N	60°55.62'W	164
22	57°49.90'N	61°21.10'W	165
23	57°57.66'N	60°43.20'W	237
24	58°01.05'N	60°32.30'W	146
28	57°08.34'N	59°29.70'W	157
30	56°53.40'N	60°34.62'W	136
36	56°04.35'N	58°54.42'W	420
38	55°46.35'N	57°13.56'W	622
39	55°33.00'N	57°50.95'W	135
40	55°27.50'N	58°00.42'W	85
41	55°20.00'N	58°29.82'W	560
78	54°47.23'N	56°59.41'W	109
79	54°52.98'N	56°29.78'W	164
80	55°02.48'N	55°40.12'W	255
84	54°18.83'N	54°24.00'W	178
85	54°12.80'N	55°15.00'W	152
87	54°07.86'N	55°43.69'W	219
88	53°05.90'N	55°29.30'W	140
89	53°15.38'N	54°54.97'W	285
90	53°26.01'N	54°20.71'W	166
91	53°37.47'N	53°33.42'W	201
94	52°42.88'N	52°47.75'W	225
1526	47°28.97'N	56°24.82'W	375
1528	47°29.02'N	56°25.21'W	330
1529	47°29.09'N	56°25.32'W	305

Table 2. Foraging attributes of polychaetes families from the Labrador continental shelf and slope and Hermitage Channel. See text for details.

FAMILY	FORAGING ATTRIBUTE		
	FEEDING TYPE	FEEDING STRATUM	MOTILITY PATTERN
Ampharetidae	microphage	surface	sessile
Apistobranchidae	microphage	surface	discretely motile
Arenicolidae	microphage	surface	discretely motile
Capitellidae (Capitella)	microphage	surface	motile
Capitellidae (others)	microphage	subsurface	motile
Chaetopteridae	microphage	surface	sessile
Cirratulidae (Cirratulus)	microphage	surface	motile
Cirratulidae (others)	microphage	subsurface	motile
Cossuridae	microphage	subsurface	motile
Dorvilleidae (in part)	macrophage	surface	motile
Dorvilleidae (in part)	microphage	surface	motile
Eunicidae	macrophage	surface	discretely motile
Flabelligeridae	microphage	surface	discretely motile
Glyceridae	macrophage	surface	discretely motile
Goniadidae	macrophage	surface	discretely motile
Lumbrineridae (in part)	macrophage	surface	motile
Lumbrineridae (in part)	microphage	surface	motile
Maldanidae	microphage	subsurface	sessile
Nephtyidae	macrophage	surface	motile
Nereidae	macrophage	surface	motile
Onuphidae	macrophage	surface	motile
Opheliidae	microphage	subsurface	motile
Orbiniidae	microphage	subsurface	motile
Oweniidae (Owenia fusiformis)	microphage	water-surface	discr. motile-sessile
Oweniidae (others)	microphage	subsurface	sessile
Paraonidae	microphage	surface	motile
Pectinidae	microphage	subsurface	motile
Phyllodocidae	macrophage	surface	motile
Pilargiidae	macrophage	surface	motile
Polynoidae	macrophage	surface	motile
Sabellidae (Fabricinae)	microphage	water	discretely motile
Sabellidae (Sabellinae)	microphage	water	sessile
Scalibregmidae	microphage	subsurface	motile
Serpulidae	microphage	water	sessile
Sigalionidae	macrophage	surface	motile
Sphaerodoridae	microphage	subsurface	motile
Spionidae	microphage	water-surface	discr. motile-sessile
Syllidae (Sphaerosyllis)	microphage	surface	motile
Syllidae (others)	macrophage	surface	motile
Terebellidae (Polycirrinae)	microphage	surface	discretely motile
Terebellidae (others)	microphage	surface	sessile
Trichobranchidae	microphage	surface	sessile
Trochochaetidae	microphage	surface	discretely motile

Table 3. Environmental variables for the sampling sites on the Labrador continental shelf and slope and in Hermitage Channel (labels used in analyses are in capitals). Asterisk indicates multicollinear variables. See text for details.

Station latitude	NEWLAT
Water depth (m)	DEPTH
Distance from shore (km)	SHORE
Distance from 200 m isobath (km)	200M
Distance from 2000 m isobath (km)	2000M
% clay in sediment	CLAY
% silt in sediment	SILT
% sand in sediment *	SAND
% gravel in sediment	GRAVEL
Average water temperature (°C)	PREDTEMP
Average range in water temperature (°C) *	TEMPRANG
Average salinity (‰) *	PREDSALI
Average range in salinity (‰) *	SALIRANG
Water current regime	CURRENT
Polychaete biomass	POLYWT
Total macrofaunal biomass	TOTALWT

Table 4. Proportion of variance explained by the unconstrained axes of Principal Components Analysis (PCA) and the constrained axes of Redundancy Analysis (RDA) in the functional and taxonomic approaches based on abundance data.

Approach	no. of var.	T.S.S.[1]	Analysis	Axis 1	Axis 2	Axis 3	Axis 4	Trace
FE	2	51.11	PCA	0.866	0.134	-	-	1.000
			RDA	0.543**	0.066	-	-	0.609**
MI	4	114.47	PCA	0.719	0.120	0.093	0.068	1.000
			RDA	0.449**	0.052	0.035	0.027	0.563**
MO	4	108.62	PCA	0.738	0.131	0.083	0.048	1.000
			RDA	0.475**	0.067	0.042	0.020	0.604**
SZ	6	130.06	PCA	0.652	0.157	0.086	0.057	1.000
			RDA	0.412**	0.092	0.040	0.027	0.587**
FORASZ	38	611.97	PCA	0.393	0.111	0.075	0.060	1.000
			RDA	0.243**	0.064	0.049	0.036	0.496**
TX	36	611.61	PCA	0.323	0.127	0.115	0.057	1.000
			RDA	0.200**	0.094	0.074	0.039	0.508*

[1] Total sum of squares in abundance data.

Significance of Axis-Environment relationship from Monte Carlo tests:

** $p \leq 0.01$

* $0.01 < p < 0.05$

Table 5. Proportion of variance explained by the unconstrained axes of Principal Components Analysis (PCA) and the constrained axes of Redundancy Analysis (RDA) in the functional and taxonomic approaches based on percentage data.

Approach	no. of var.	T.S.S.[1]	Analysis	Axis 1	Axis 2	Axis 3	Axis 4	Trace
FE	2	0.97	PCA	1.000	-	-	-	1.000
			RDA	0.561*	-	-	-	0.561*
MI	4	1.63	PCA	0.501	0.357	0.142	-	1.000
			RDA	0.205n.s.	0.093	0.055	-	0.353n.s.
MO	4	2.09	PCA	0.660	0.239	0.101	-	1.000
			RDA	0.476**	0.131	0.056	-	0.664**
SZ	6	1.64	PCA	0.455	0.311	0.199	0.030	1.000
			RDA	0.351**	0.212	0.089	0.008	0.662**
FORASZ	38	2.78	PCA	0.205	0.157	0.139	0.099	1.000
			RDA	0.147**	0.117	0.086	0.040	0.516**
TX	36	3.43	PCA	0.201	0.166	0.149	0.140	1.000
			RDA	0.117**	0.113	0.102	0.046	0.509n.s.

[1] Total sum of squares in percentage data.

Significance of Axis-Environment relationship from Monte Carlo tests:

** $p \leq 0.01$

* $0.01 < p < 0.05$

n.s. not significant ($p > 0.05$)

Figure 1. Location of sampling sites on the Labrador continental shelf and slope and in Hermitage Channel, Newfoundland.

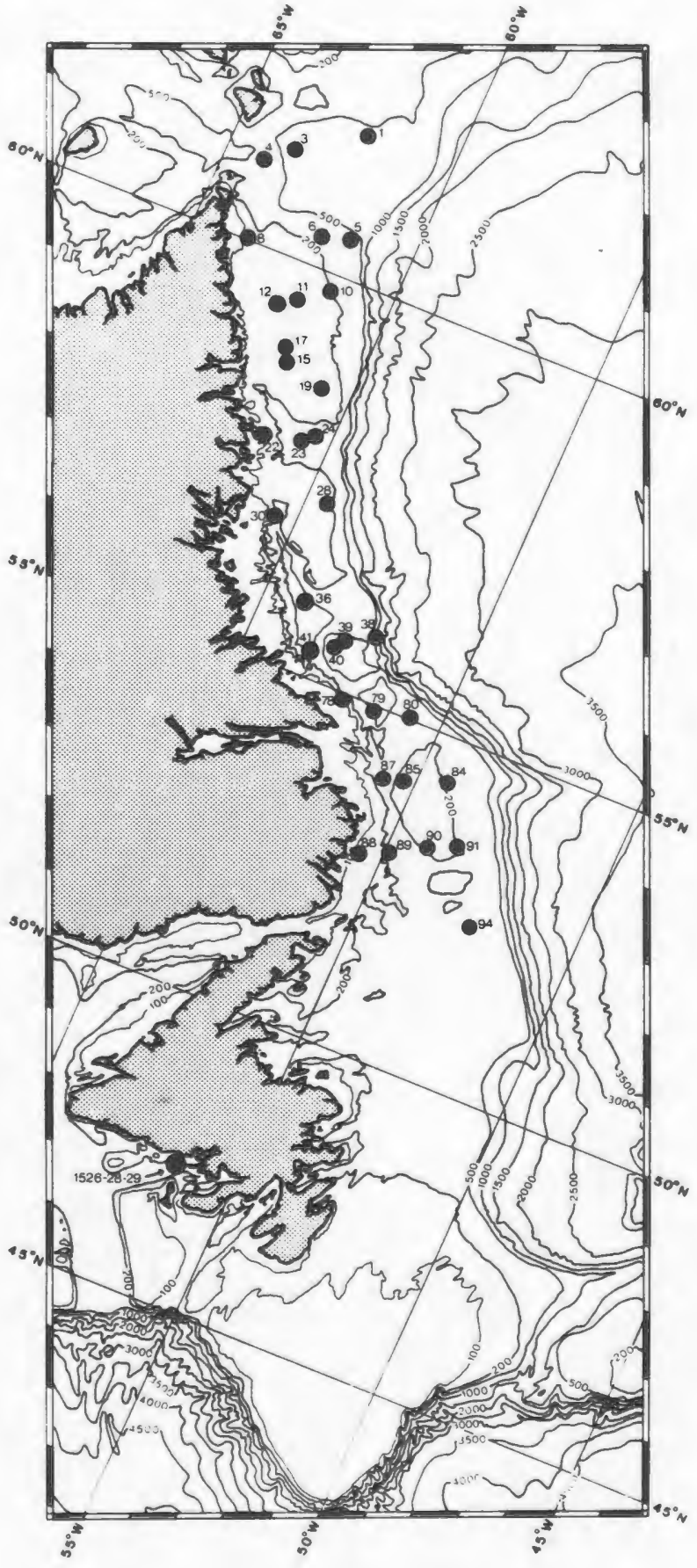

65°W
60°W
60°N
55°N
50°N
45°N
55°W
50°W
45°W
1526-28-29

Figure 2. Summary of the different combinations between the biological attributes (foraging attributes and body size), excluding taxon.

FEEDING TYPE	FEEDING STRATUM (MICROHABITAT)	MOTILITY PATTERN	BODY SIZE CLASS
Microphage	water	sessile	1–4
		discretely motile	1–4
	sediment surface	sessile	1–4
		discretely motile	1–4
		motile	1–4
	sediment subsurface	sessile	1–4
		motile	1–4
	water / sediment surface	sessile / discretely motile	1–4
Macrophage	sediment surface	discretely motile	1–4
		motile	1–4

Figure 3. Observed body length versus maximum diameter of invividual macrobenthic polychaetes belonging to the families Sabellidae, Cirratulidae (*Chaetozone* sp.) and Spionidae. Full line represents estimated length/diameter relationship of non-truncated specimens. Dashed line represents cut-off point below which the speciment length is corrected to fit the estimated (non-truncated) length for a given diameter.

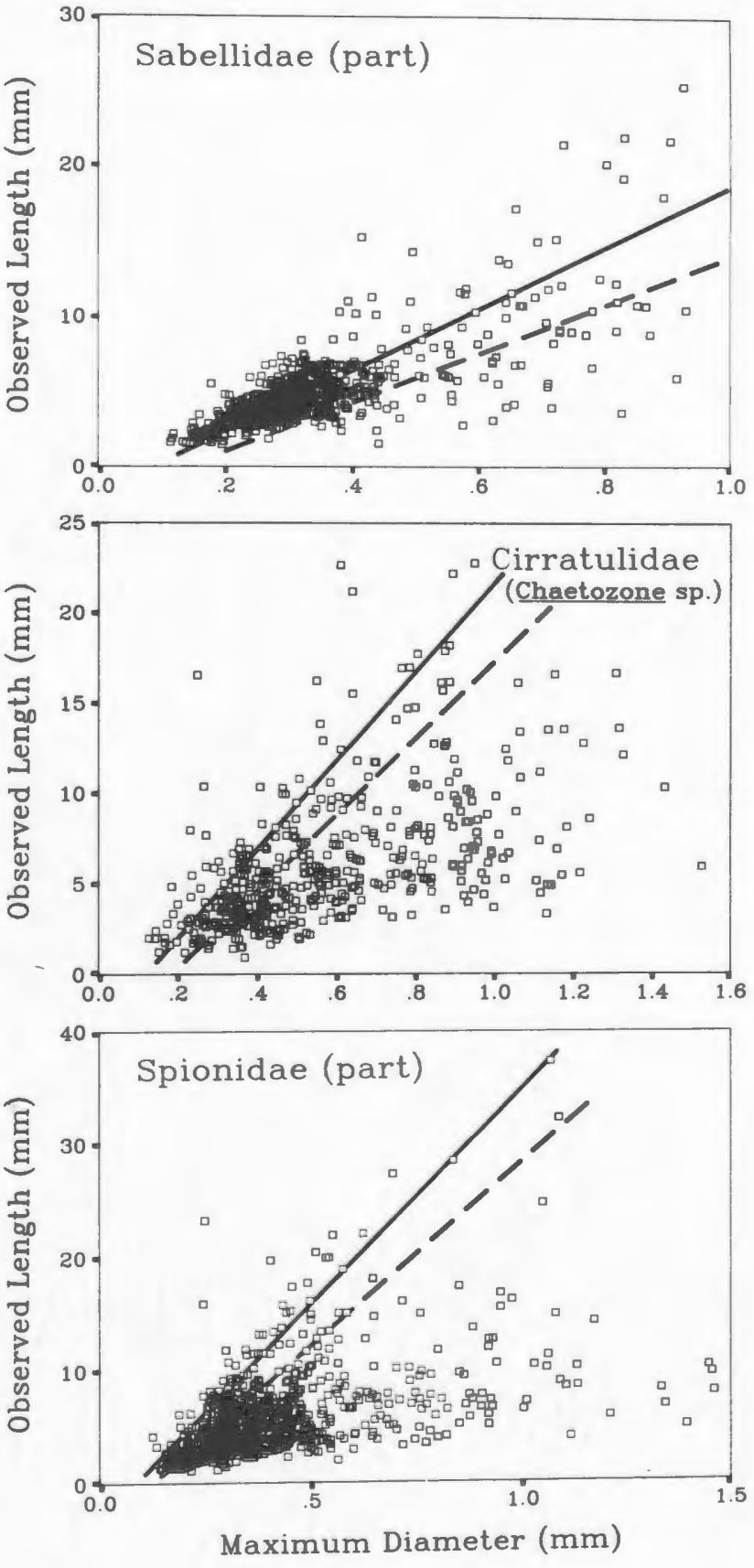

Sabellidae (part)
Observed Length (mm)
30
20
10
0
0.0
.2
.4
.6
.8
1.0
Cirratulidae
(Chaetozone sp.)
Observed Length (mm)
25
20
15
10
5
0
0.0
.2
.4
.6
.8
1.0
1.2
1.4
1.6
Spionidae (part)
Observed Length (mm)
40
30
20
10
0
0.0
.5
1.0
1.5
Maximum Diameter (mm)

Figure 4. Ternary diagram of mud (silt-clay), sand and gravel proportions in grab samples from the Labrador Shelf and Slope and Hermitage Channel. Data points are labelled with the station number as listed in Table 1.

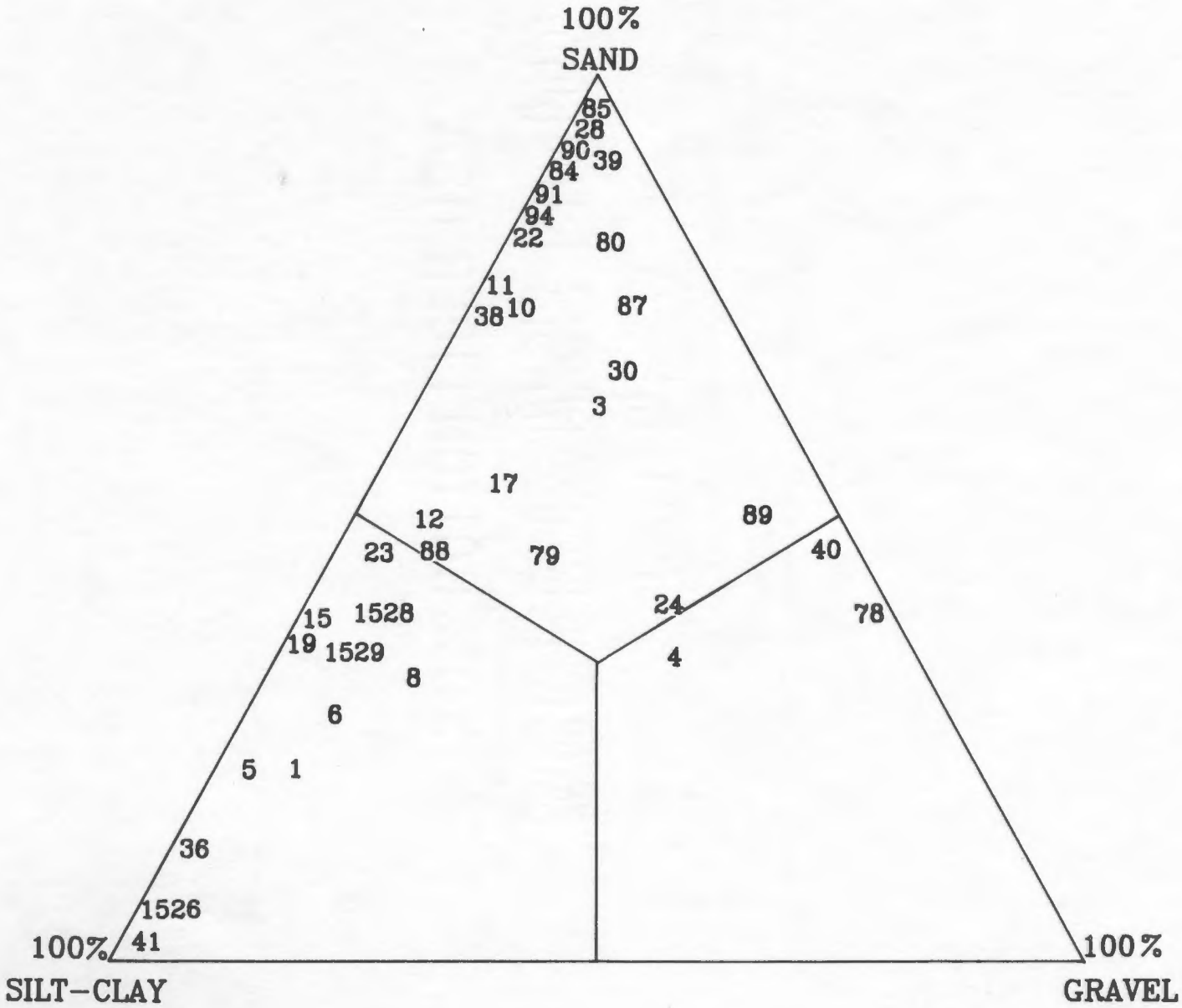

100%
SAND
85
28
90
39
84
91
94
22
80
11
38
10
87
30
3
17
12
89
23
88
79
40
24
15
1528
78
19
1529
4
8
6
5
1
36
1526
41
100%
SILT-CLAY
100%
GRAVEL

Figure 5. Absolute frequencies of macrophage and microphage polychaetes in grab samples from the Labrador continental shelf and slope and Hermitage Channel. Data points are labelled with the station number as listed in Table 1.

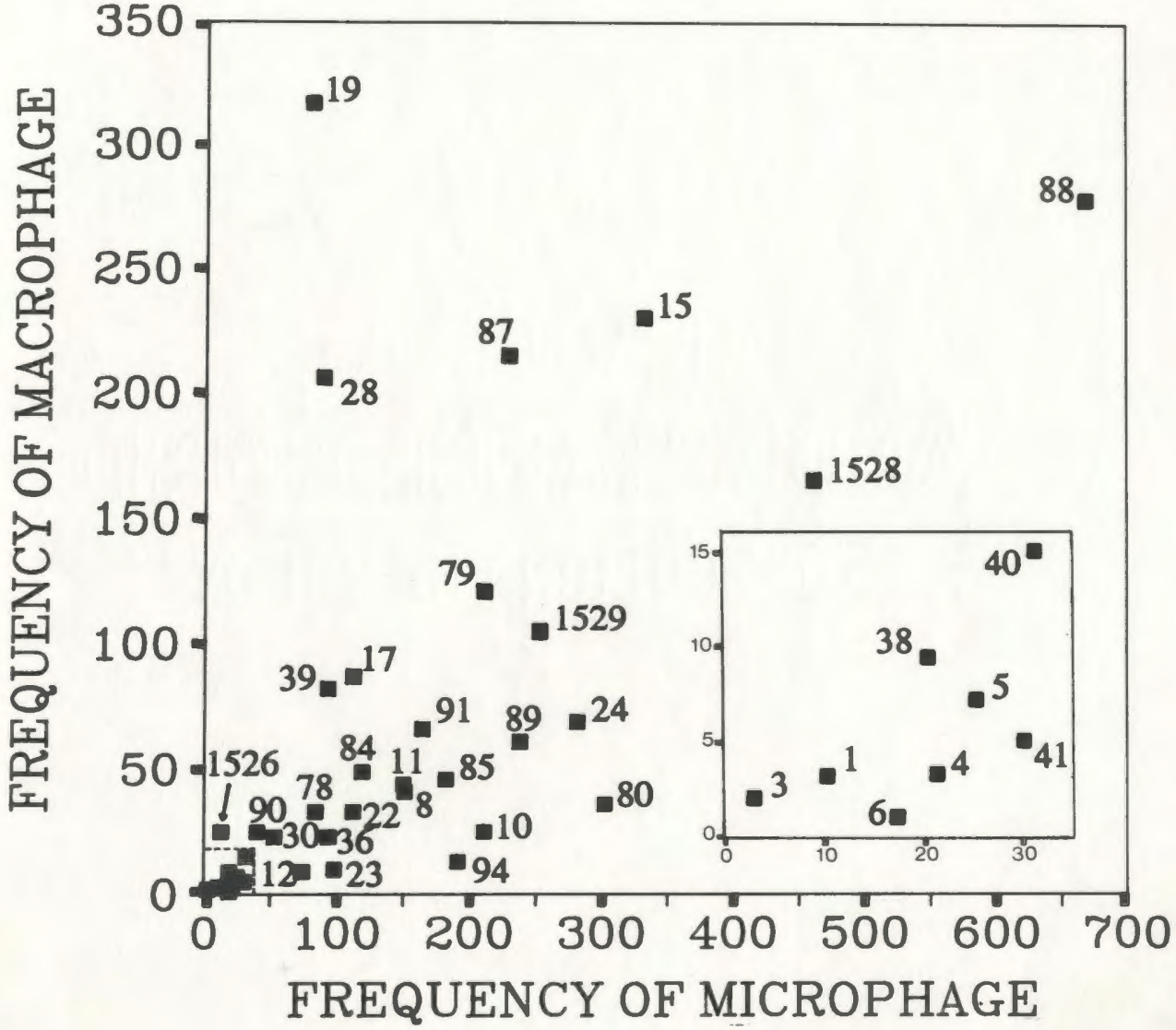

FREQUENCY OF MACROPHAGE
FREQUENCY OF MICROPHAGE
0
50
100
150
200
250
300
350
0
100
200
300
400
500
600
700
19
88
15
87
28
1528
79
1529
39
17
91
89
24
84
11
85
1526
78
8
80
90
22
10
30
36
12
23
94
40
38
5
41
1
4
3
6
0
5
10
15
0
10
20
30

Figure 6. Transformed (√√) absolute frequencies of macrophage and microphage polychaetes in grab samples from the Labrador continental shelf and slope and Hermitage Channel. UPGMA groupings are represented by the envelopes around the samples. Data points are labelled with the station number as listed in Table 1.

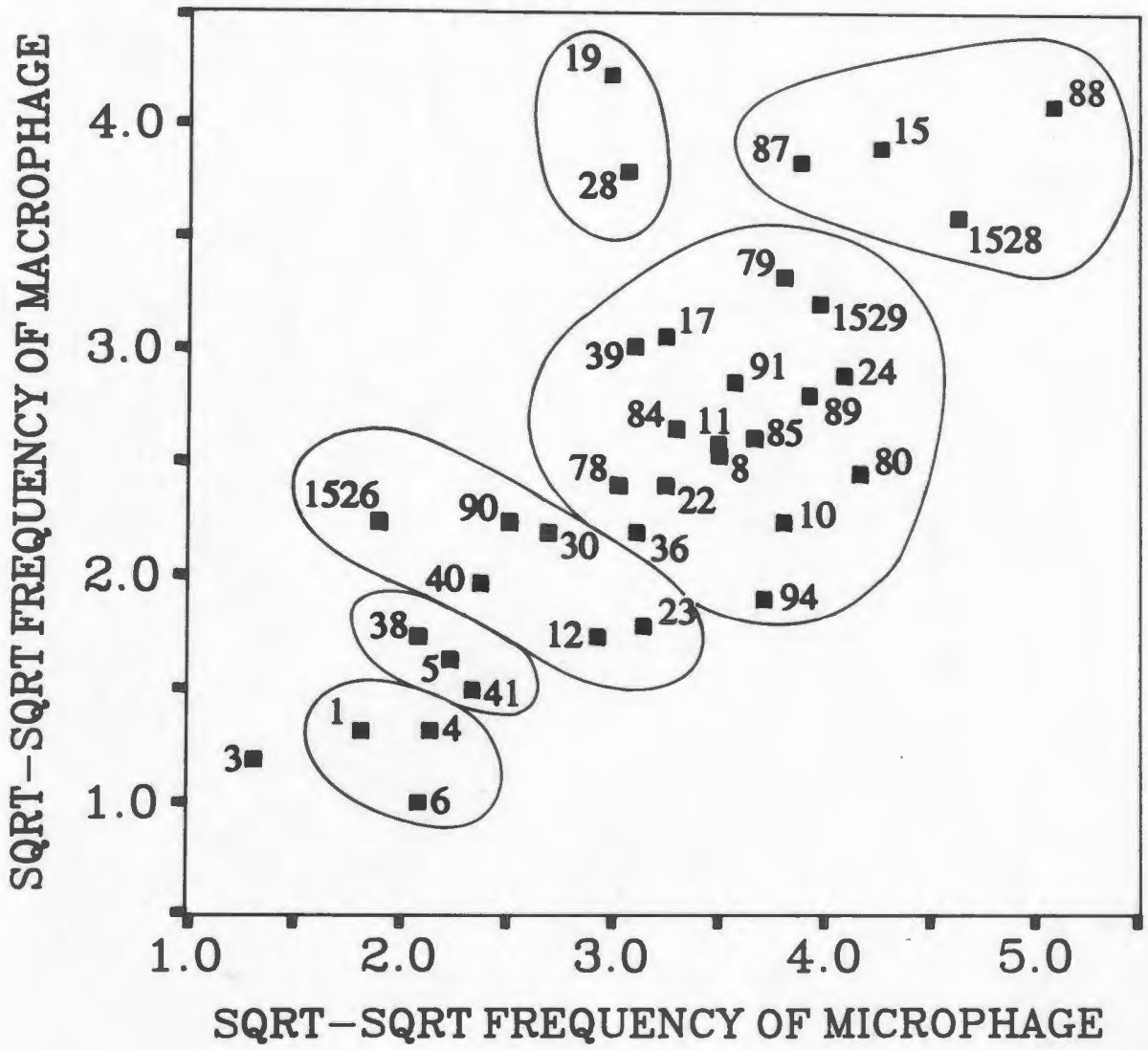

SQRT−SQRT FREQUENCY OF MACROPHAGE
4.0
3.0
2.0
1.0
19
28
88
87
15
1528
79
1529
17
39
91
24
84
11
85
89
78
8
80
1526
90
22
10
30
36
40
94
38
12
23
5
41
1
4
3
6
1.0
2.0
3.0
4.0
5.0
SQRT−SQRT FREQUENCY OF MICROPHAGE

Figure 7. Multidimensional scaling ordination of samples based on the **feeding type** approach, using √√-transformed abundance data (stress value for two dimensions: 0.07). UPGMA groupings are represented by the envelopes around the samples. Data points are labelled with the station number as listed in Table 1.

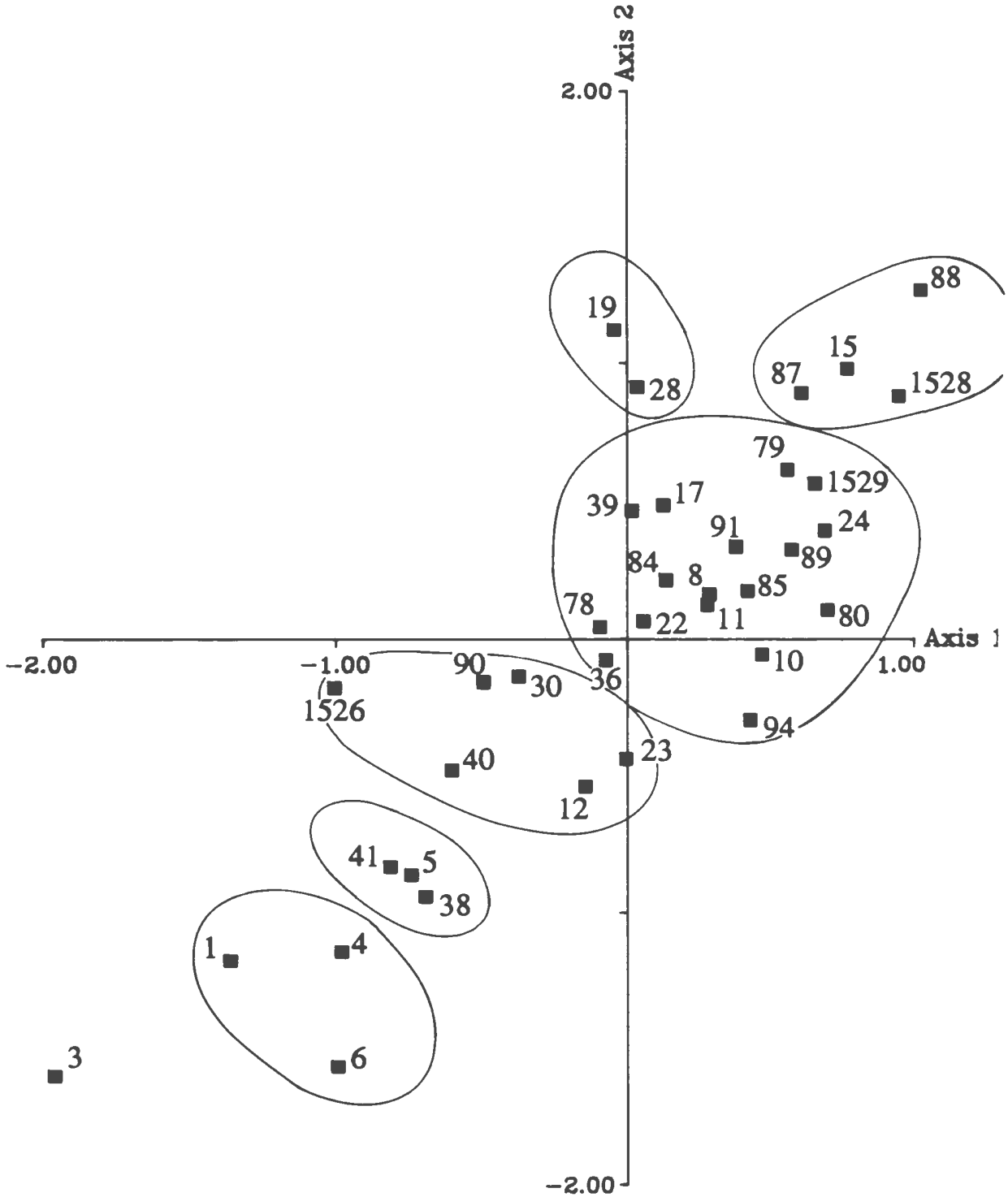

Axis 2
2.00
-2.00
Axis 1
-2.00
-1.00
1.00
19
28
88
15
87
1528
79
1529
39
17
91
24
89
84
8
85
78
22
11
80
10
90
30
36
1526
94
40
23
12
41
5
38
1
4
3
6

Figure 8. Principal Components Analysis for the **feeding type** approach, using √√-transformed abundance data. Sample points (■) are labelled with station numbers (see Table 1) and biological variables (●) with lowercase alphanumeric codes. See Figure 2 for explanation of variable codes. Variables situated outside the range of sample points in the ordination are indicated by a small arrow next to the variable code.

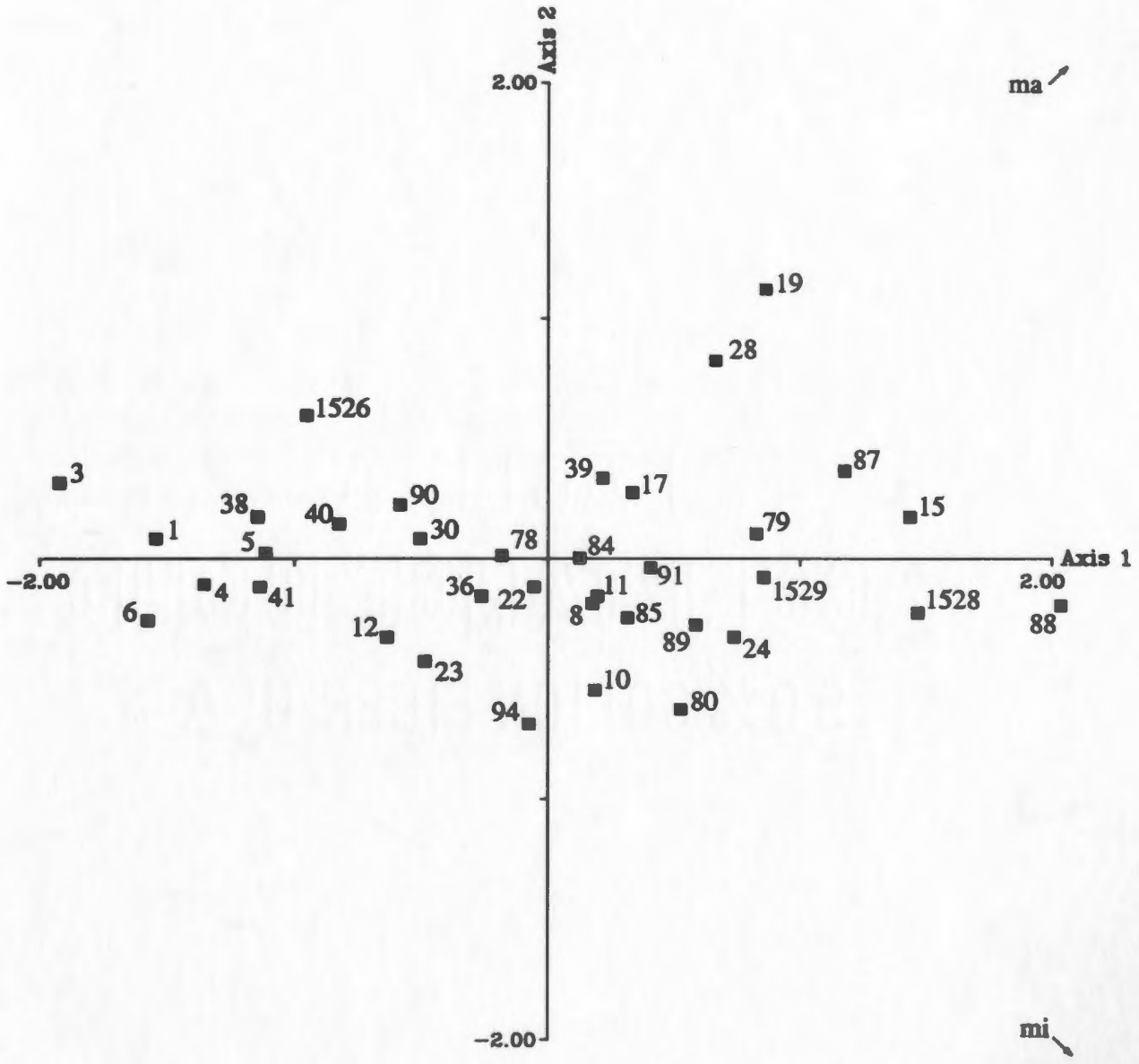

Axis 2
2.00
-2.00
Axis 1
2.00
-2.00
ma
mi
19
28
1526
3
39
17
87
38
40
90
15
1
30
79
5
78
84
91
4
41
36
22
11
1529
1528
6
8
85
88
12
89
24
23
10
94
80

Figure 9. Redundancy Analysis for the **feeding type** approach, using $\sqrt{\sqrt{\ }}$-transformed abundance data. Sample points (■) are labelled with station numbers (see Table 1), biological variables (●) with lowercase alphanumeric codes (see Figure 2 for explanation of variable codes), and environmental variables (↦) with uppercase labels (abbreviation of variable name). Biological variables situated outside the range of sample points in the ordination are indicated by a small arrow next to the variable code. Scaling factor of environmental biplot scores= 3.96.

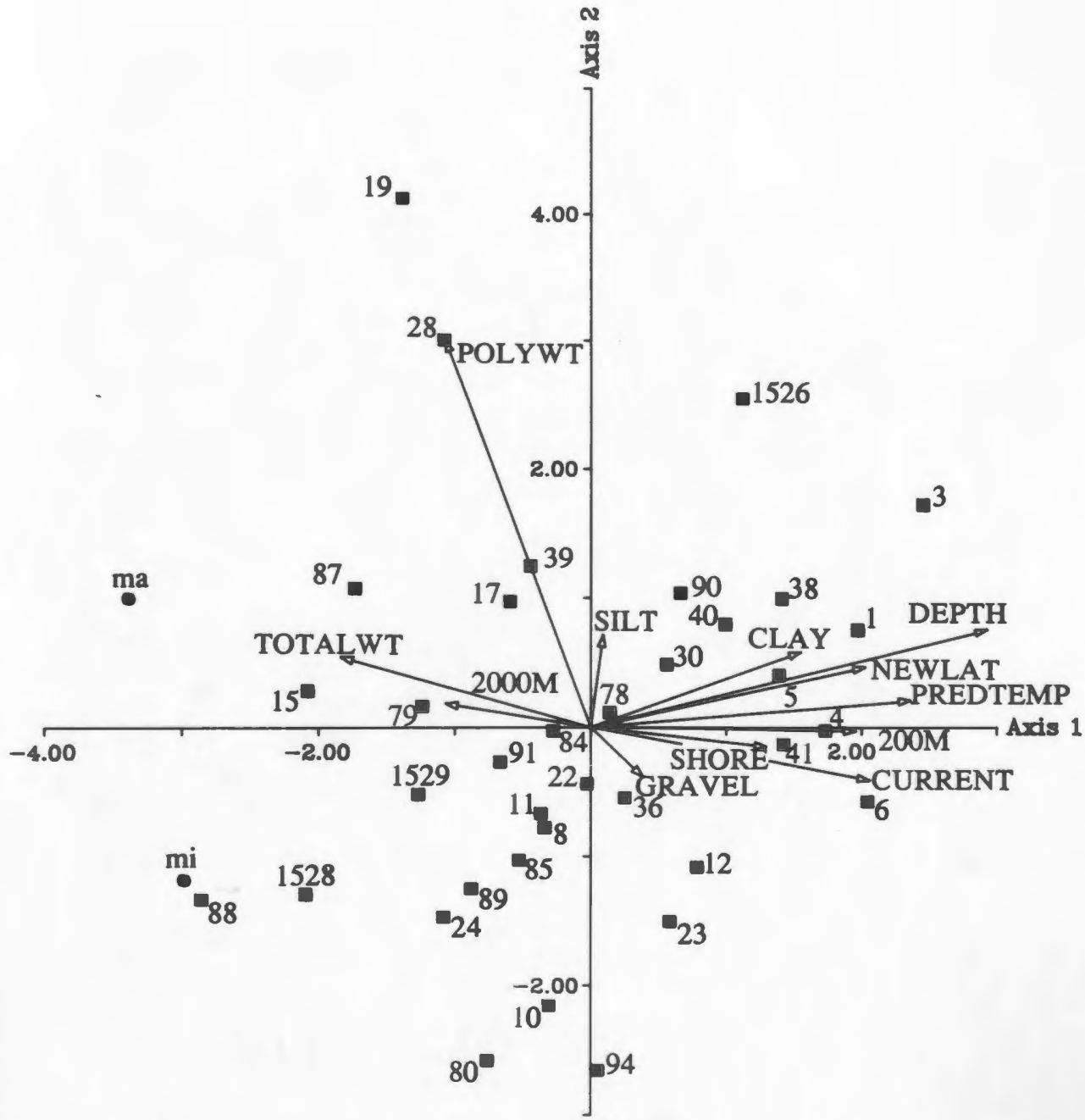

Axis 2
Axis 1
4.00
2.00
-2.00
-4.00
-2.00
2.00
19
28
POLYWT
1526
3
39
ma
87
17
90
38
40
SILT
CLAY
1
DEPTH
TOTALWT
30
NEWLAT
2000M
15
79
78
5
PREDTEMP
4
84
91
41
200M
SHORE
1529
22
GRAVEL
CURRENT
36
11
6
8
mi
1528
85
12
89
88
24
23
10
80
94

Figure 10. Cumulative proportion of variance explained by the first four axes and by all axes (trace) of Principal Components Analysis and Redundancy Analysis for the **feeding type** approach, using $\sqrt{\sqrt{\ }}$-transformed abundance data.

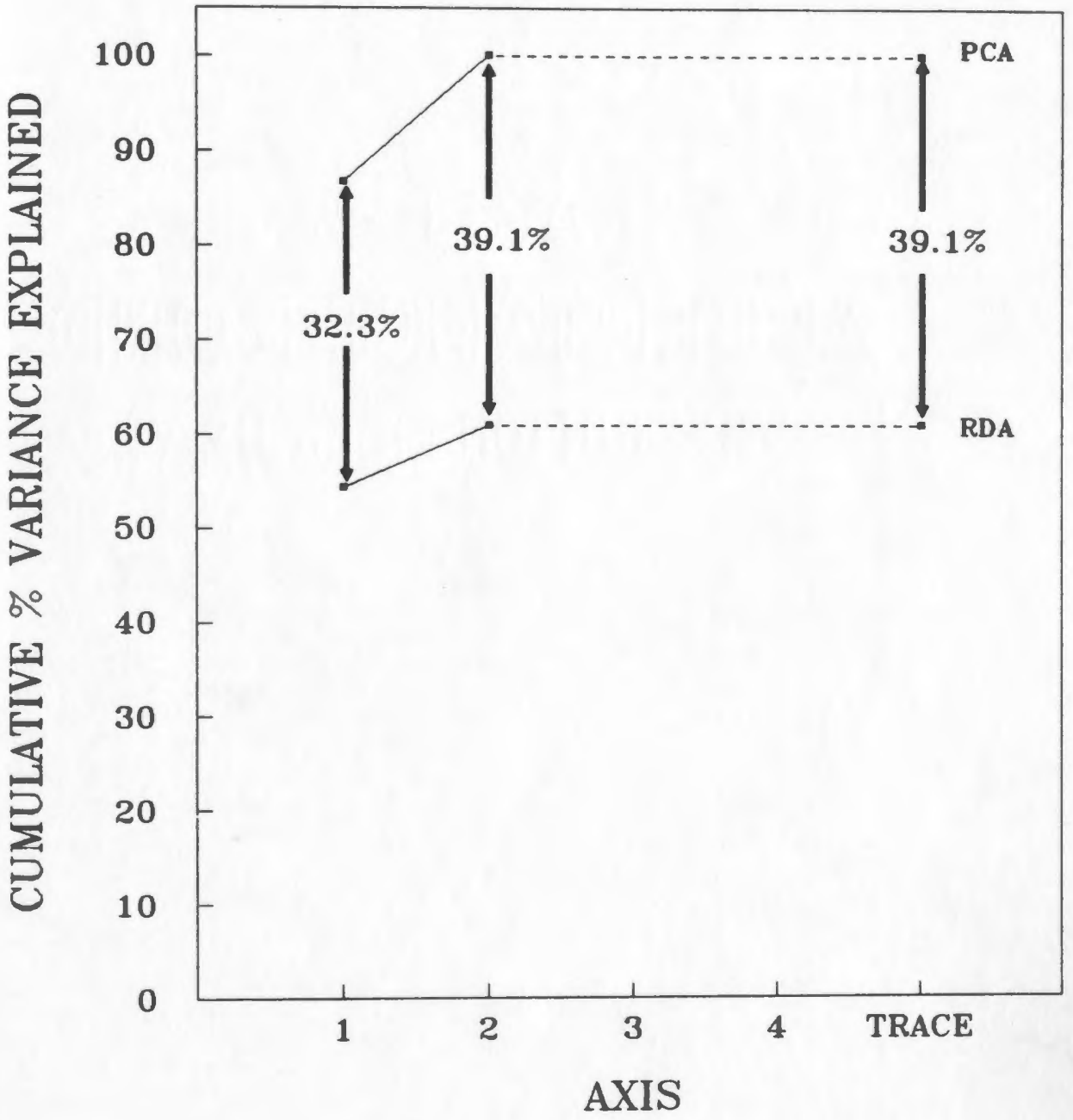

CUMULATIVE % VARIANCE EXPLAINED
100
90
80
70
60
50
40
30
20
10
0
PCA
RDA
32.3%
39.1%
39.1%
1
2
3
4
TRACE
AXIS

Figure 11. Proportions of macrophage and microphage polychaetes in grab samples. UPGMA groupings are represented by the envelopes around the samples. Data points are labelled with the station number as listed in Table 1.

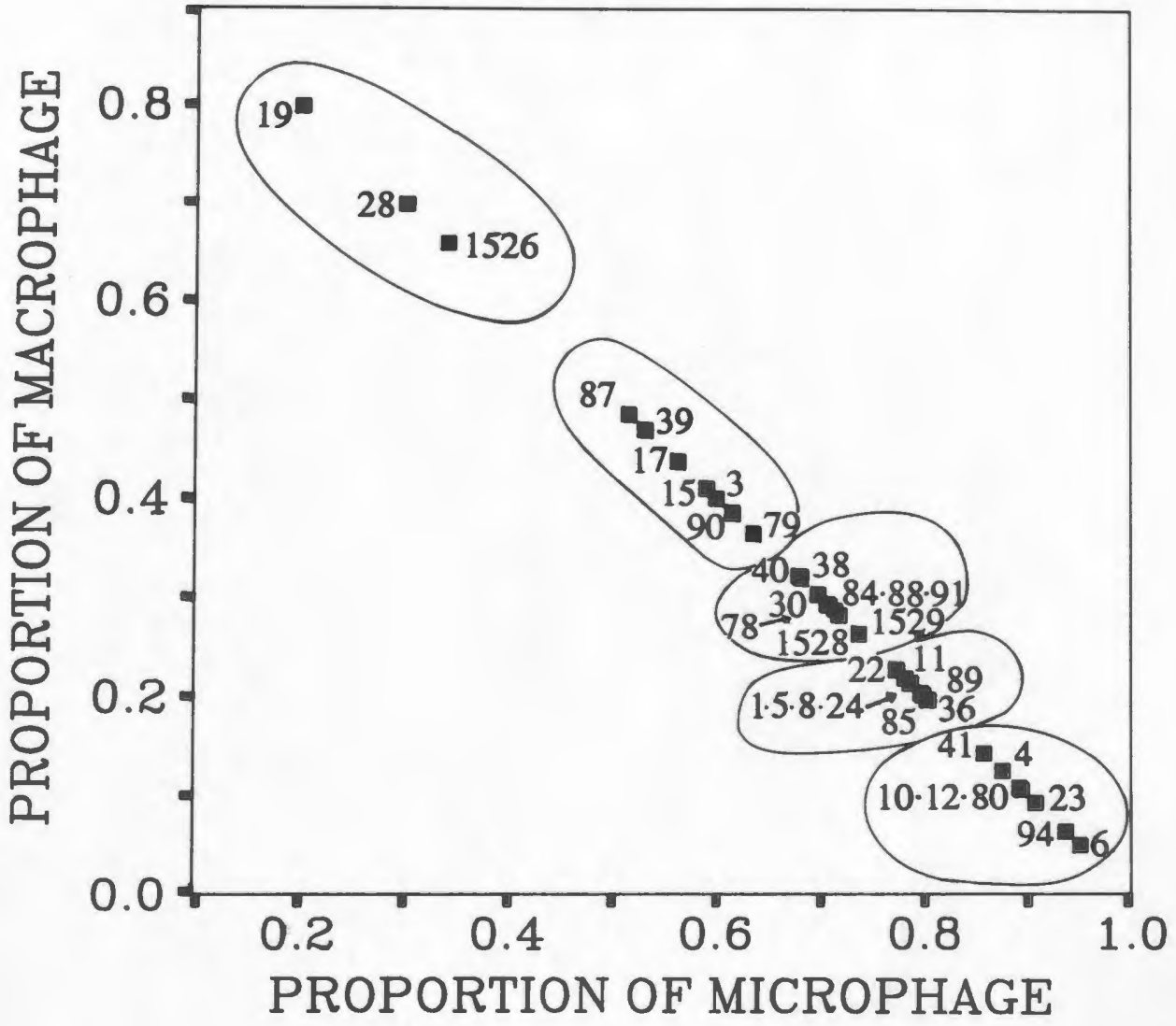

PROPORTION OF MACROPHAGE
0.0
0.2
0.4
0.6
0.8
19
28
1526
87
39
17
15
3
90
79
40
38
84·88·91
30
78
1529
1528
22
11
89
1·5·8·24
85
36
41
4
10·12·80
23
94
6
0.2
0.4
0.6
0.8
1.0
PROPORTION OF MICROPHAGE

Figure 12. Multidimensional scaling ordination of samples based on the **feeding type** approach, using arcsin$\sqrt{}$-transformed percentage data (stress value for two dimensions: 0.003). UPGMA groupings are represented by the envelopes around the samples. Data points are labelled with the station number as listed in Table 1.

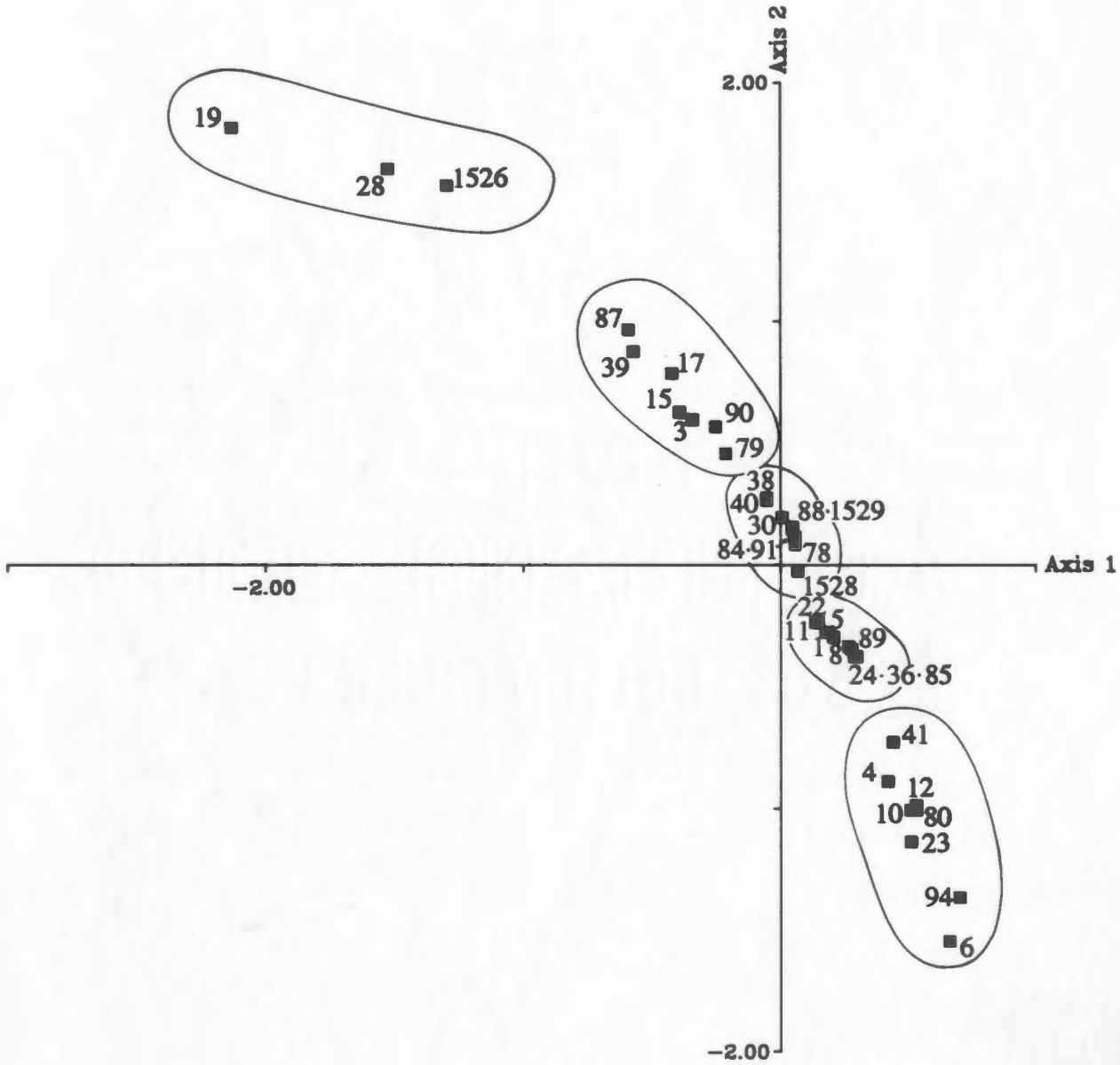

Axis 2
2.00
-2.00
Axis 1
-2.00
19
28
1526
87
39
17
15
3
90
79
38
40
88·1529
30
84·91
78
1528
22
5
11
89
18
24·36·85
41
4
12
10
80
23
94
6

Figure 13. Principal Components Analysis for the **feeding type** approach, using $\log_e$-transformed percentage data. Sample points (■) are labelled with station numbers (see Table 1) and biological variables (●) with lowercase alphanumeric codes. See Figure 2 for explanation of variable codes. Variables situated outside the range of sample points in the ordination are indicated by a small arrow next to the variable code.

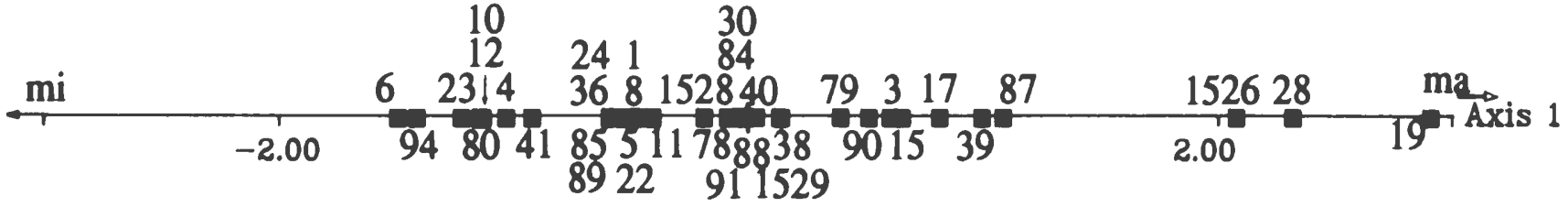

10
12
24 1
30
84
mi
6 23 14
36 8 15 28 40
79 3 17
87
1526 28
ma
Axis 1
−2.00
94 80 41 85 5 11 78 88 38 90 15 39
2.00
19
89 22
91 1529

Figure 14. Redundancy Analysis for the **feeding type** approach, using $\log_e$-transformed percentage data. Sample points (■) are labelled with station numbers (see Table 1), biological variables (●) with lowercase alphanumeric codes (see Figure 2 for explanation of variable codes), and environmental variables (↦) with uppercase labels (abbreviation of variable name). Biological variables situated outside the range of sample points in the ordination are indicated by a small arrow next to the variable code. Scaling factor of environmental biplot scores= 6.14.

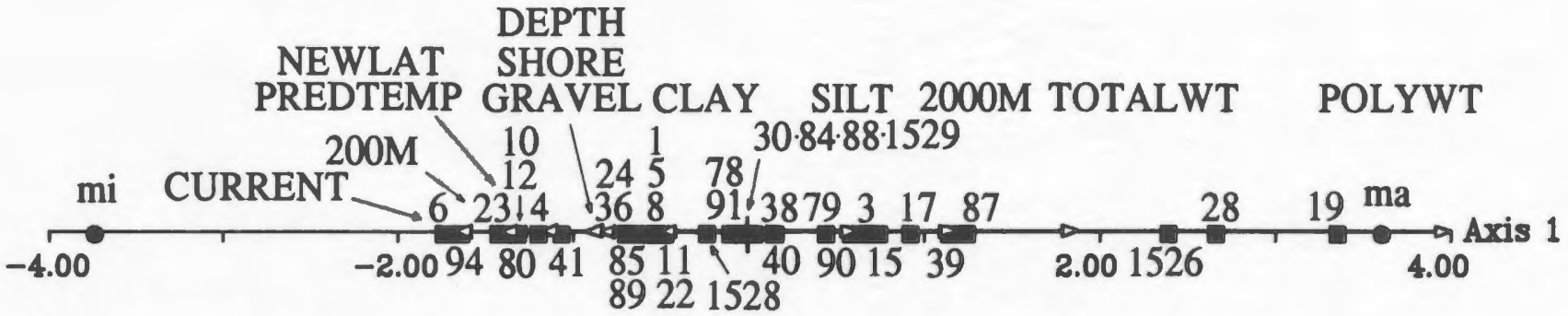

DEPTH
NEWLAT SHORE
PREDTEMP GRAVEL CLAY SILT 2000M TOTALWT POLYWT
200M
CURRENT
mi
ma
Axis 1
-4.00
-2.00
2.00
4.00
10 1 30 84 88 1529
12 24 5 78
6 23 4 36 8 91 38 79 3 17 87 28 19
94 80 41 85 11 40 90 15 39 1526
89 22 1528

Figure 15. Cumulative proportion of variance explained by the first four axes and by all axes (trace) of Principal Components Analysis and Redundancy Analysis for the **feeding type** approach, using $\log_e$-transformed percentage data.

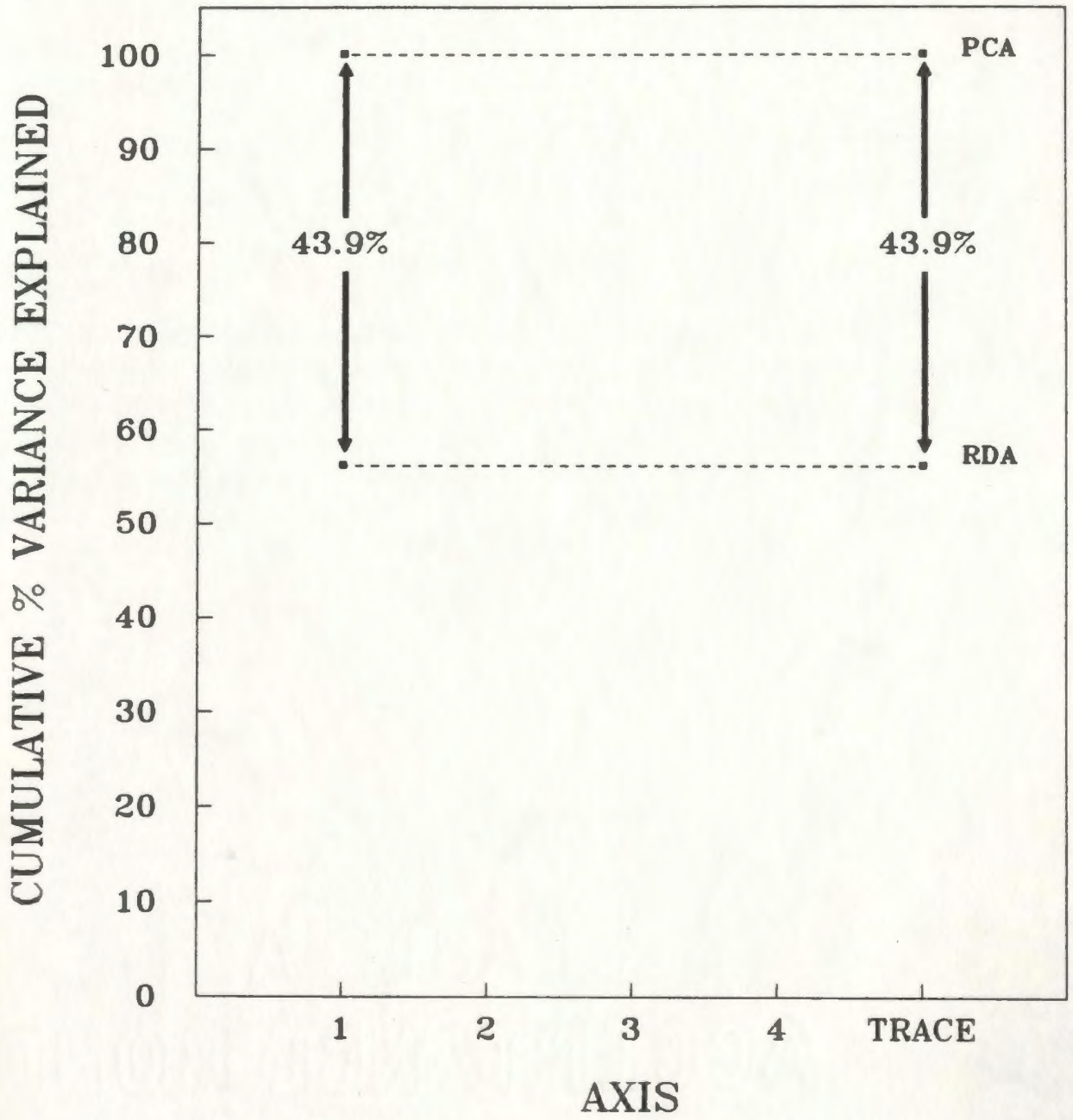

CUMULATIVE % VARIANCE EXPLAINED
100
90
80
70
60
50
40
30
20
10
0
PCA
RDA
43.9%
43.9%
1
2
3
4
TRACE
AXIS

Figure 16. Multidimensional scaling ordination of samples based on the **microhabitat** approach, using √√-transformed abundance data (stress value for two dimensions: 0.15). UPGMA groupings are represented by the envelopes around the samples. Data points are labelled with the station number as listed in Table 1.

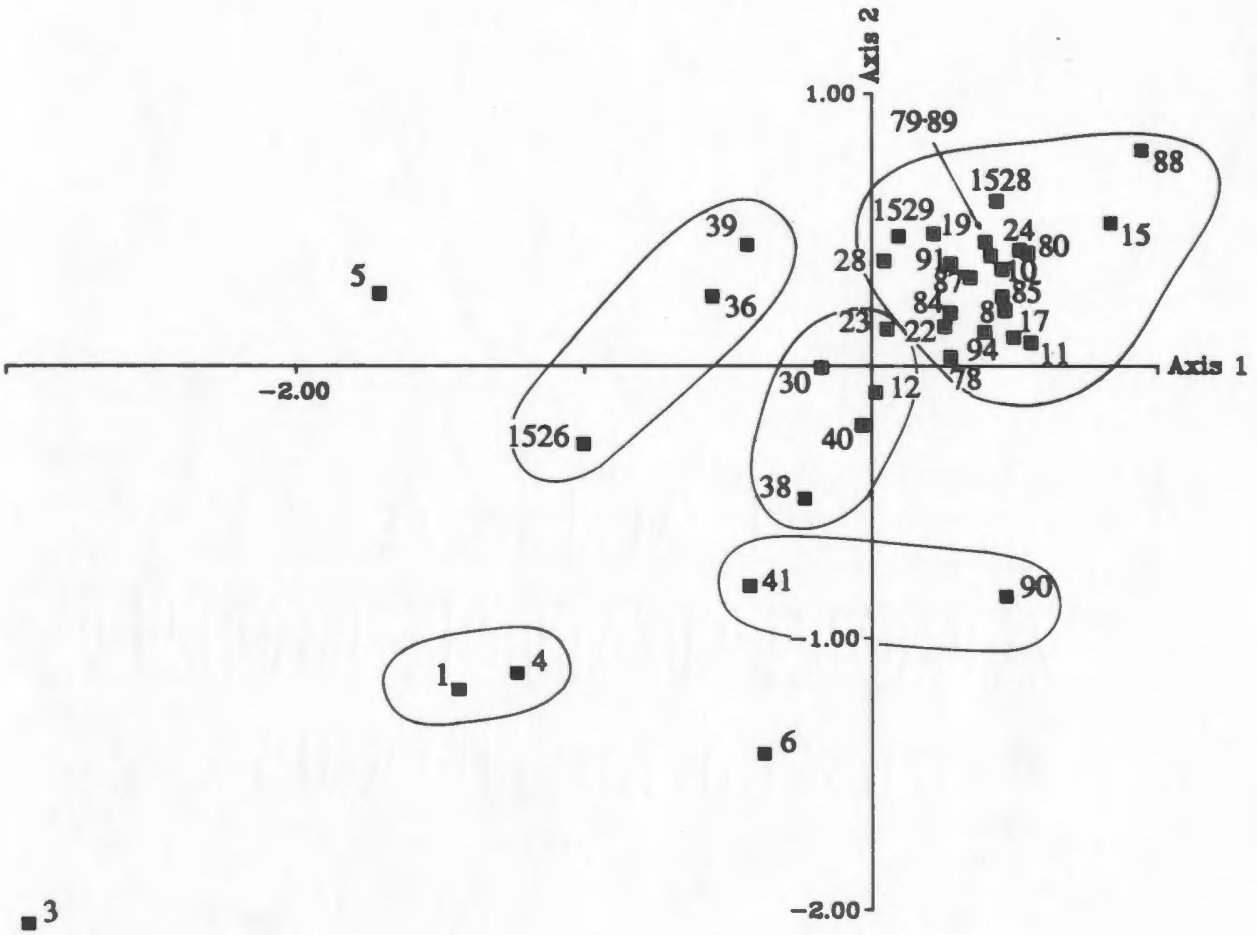

Axis 2
1.00
79-89
88
1528
1529
19
24
15
80
39
28
91
10
5
87
85
36
84
8
17
23
22
94
11
Axis 1
-2.00
30
12
78
1526
40
38
41
90
-1.00
1
4
6
3
-2.00

Figure 17. Principal Components Analysis for the **microhabitat** approach, using √√-transformed abundance data. Sample points (■) are labelled with station numbers (see Table 1) and biological variables (●) with lowercase alphanumeric codes. See Figure 2 for explanation of variable codes. Variables situated outside the range of sample points in the ordination are indicated by a small arrow next to the variable code.

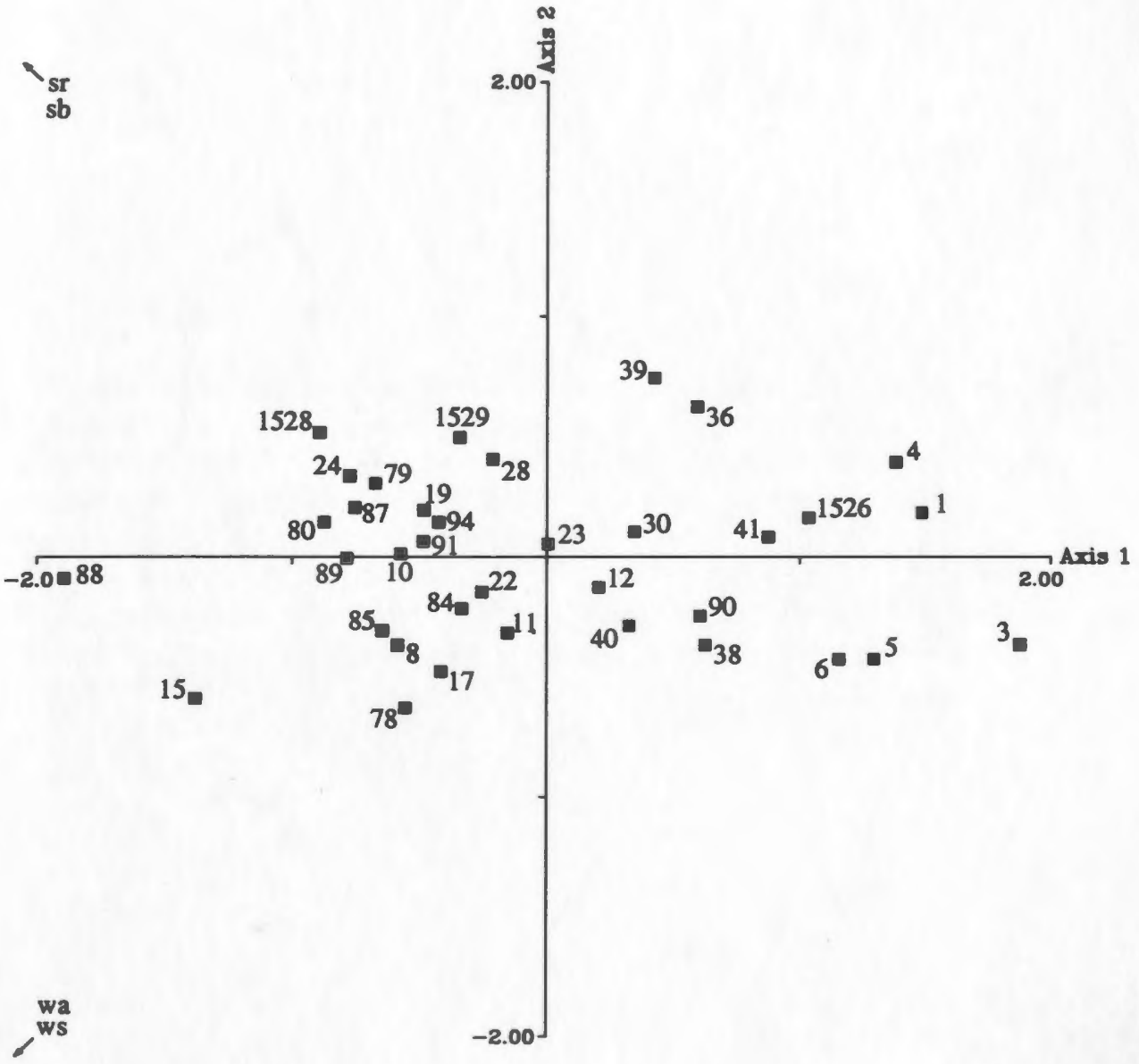

Axis 2
2.00
-2.00
Axis 1
2.00
-2.0
sr
sb
wa
ws
39
36
1528
1529
4
24
79
28
19
87
94
80
91
23
30
41
1526
1
88
89
10
22
12
84
90
85
11
40
3
8
38
5
6
17
15
78

Figure 18. Redundancy Analysis for the **microhabitat** approach, using √√-transformed abundance data. Sample points (■) are labelled with station numbers (see Table 1), biological variables (●) with lowercase alphanumeric codes (see Figure 2 for explanation of variable codes), and environmental variables (↦) with uppercase labels (abbreviation of variable name). Biological variables situated outside the range of sample points in the ordination are indicated by a small arrow next to the variable code. Scaling factor of environmental biplot scores= 3.58.

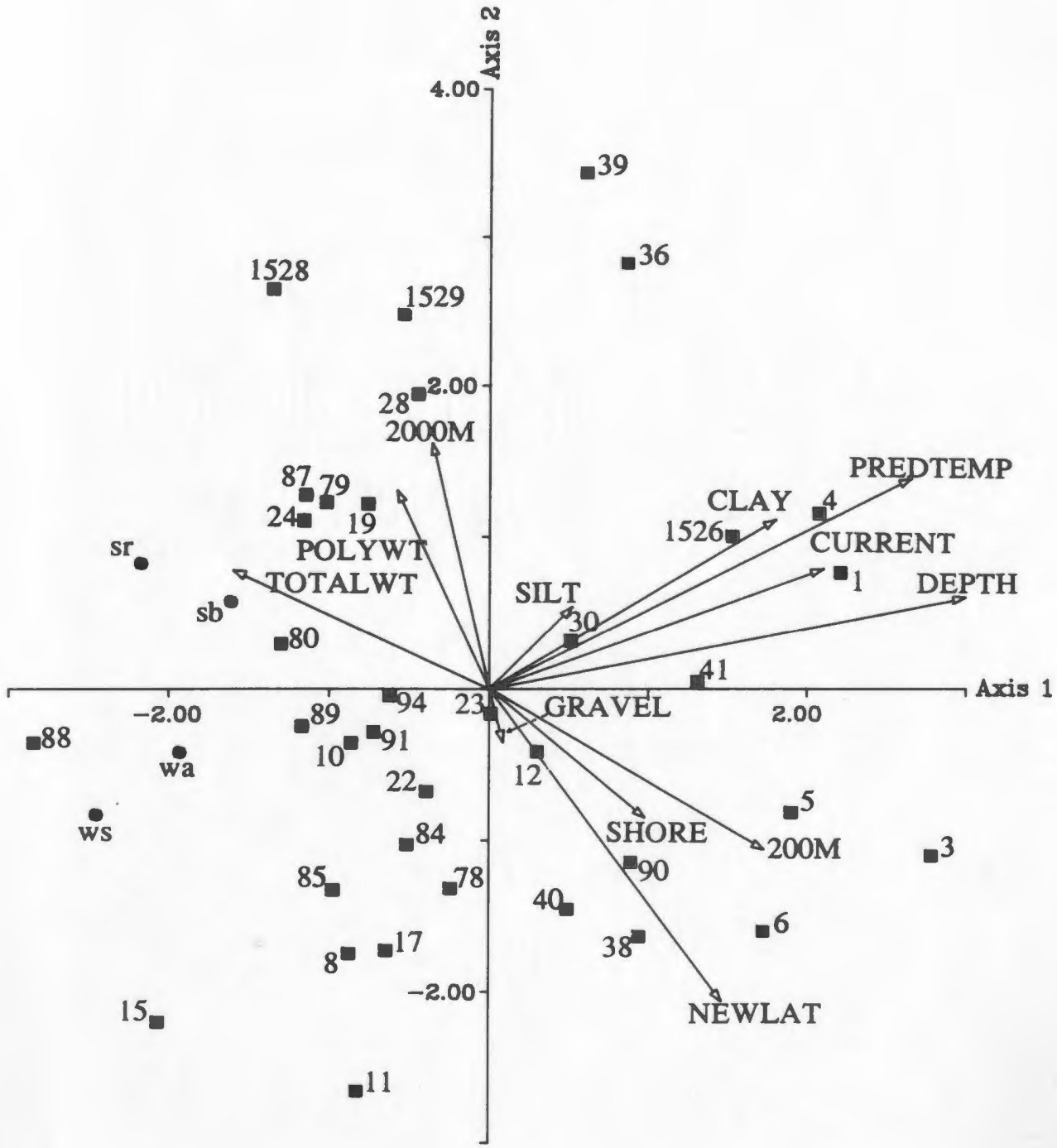

Axis 2
4.00
2.00
−2.00
Axis 1
2.00
39
36
1528
1529
28
2000M
87
79
24
19
sr
POLYWT
TOTALWT
sb
80
PREDTEMP
CLAY
4
1526
CURRENT
1
DEPTH
SILT
30
41
94
23
GRAVEL
89
91
10
88
wa
22
12
ws
84
5
SHORE
200M
3
90
85
78
40
6
38
8
17
15
NEWLAT
11

Figure 19. Cumulative proportion of variance explained by the first four axes and by all axes (trace) of Principal Components Analysis and Redundancy Analysis for the **microhabitat** approach, using √√-transformed abundance data.

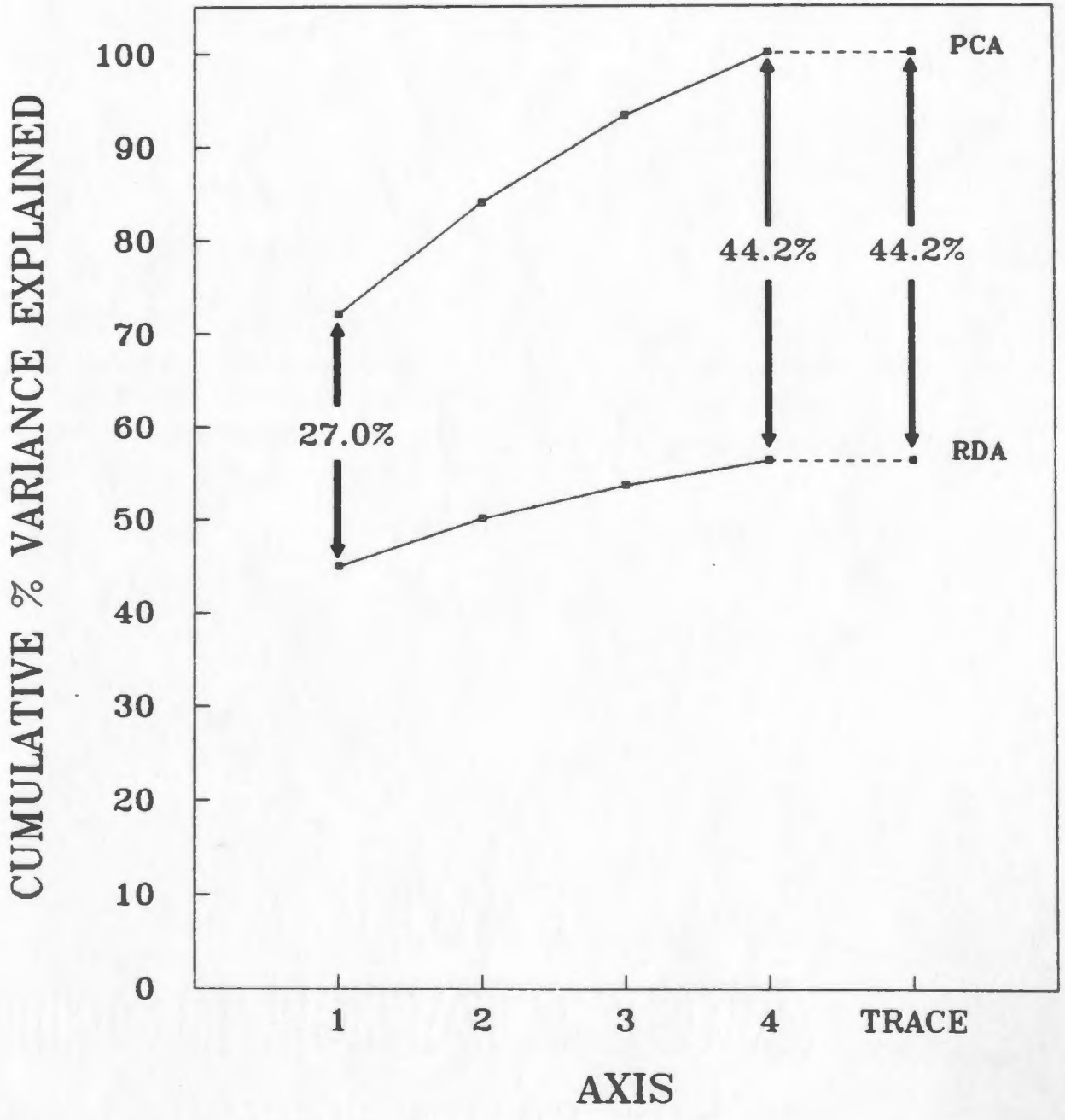

CUMULATIVE % VARIANCE EXPLAINED
100
90
80
70
60
50
40
30
20
10
0
PCA
RDA
44.2%
44.2%
27.0%
1
2
3
4
TRACE
AXIS

Figure 20. Multidimensional scaling ordination of samples based on the **microhabitat** approach, using arcsin$\sqrt{\cdot}$-transformed percentage data (stress value for two dimensions: 0.31). UPGMA groupings are represented by the envelopes around the samples. Data points are labelled with the station number as listed in Table 1.

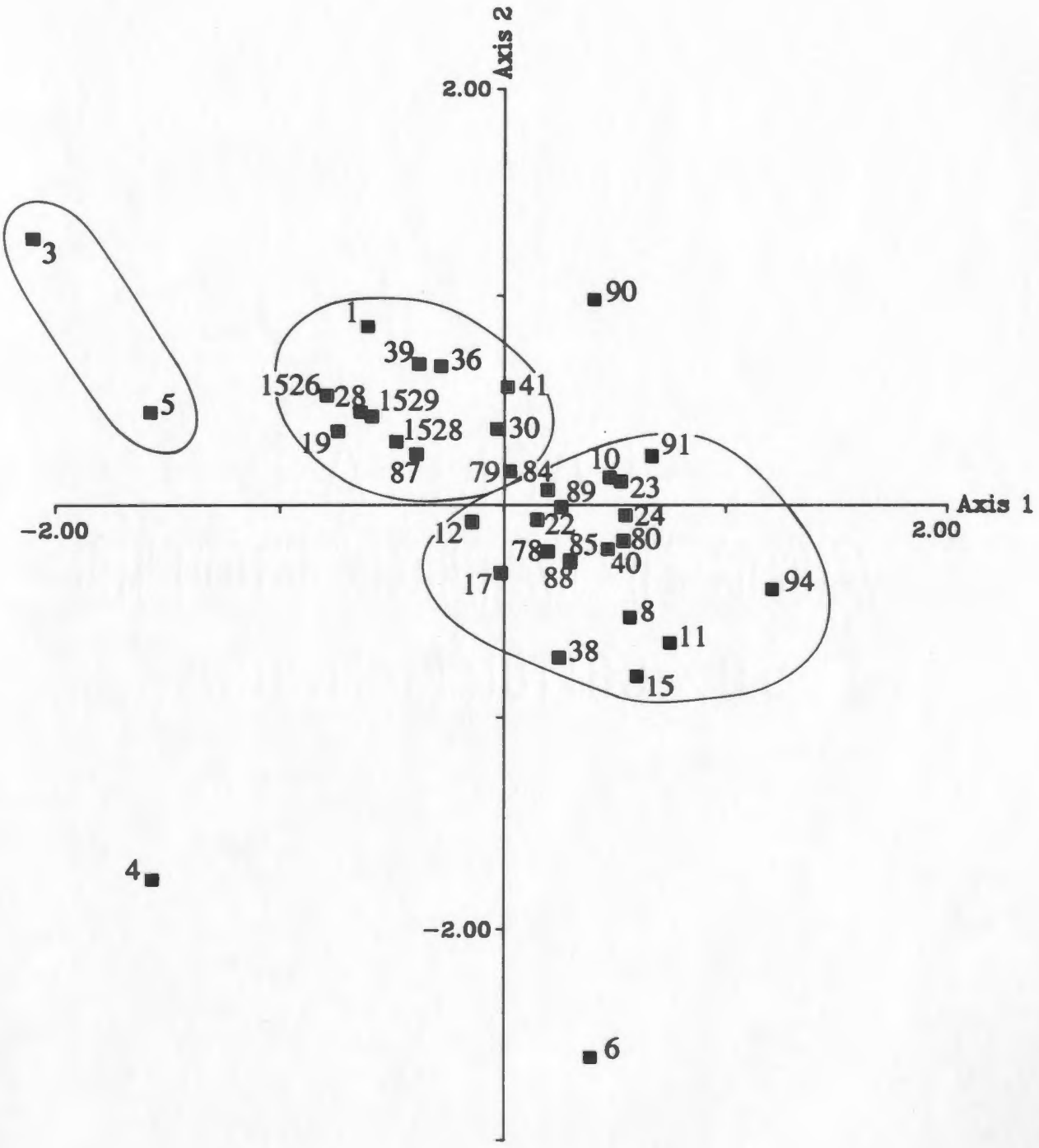

Axis 2
2.00
-2.00
Axis 1
-2.00
2.00
3
5
4
1
39
36
1526
28
1529
41
19
1528
30
87
79
84
90
91
10
23
89
24
12
22
80
78
85
40
17
88
94
8
11
38
15
6

Figure 21. Principal Components Analysis for the **microhabitat** approach, using $\log_e$-transformed percentage data. Sample points (■) are labelled with station numbers (see Table 1) and biological variables (●) with lowercase alphanumeric codes. See Figure 2 for explanation of variable codes. Variables situated outside the range of sample points in the ordination are indicated by a small arrow next to the variable code.

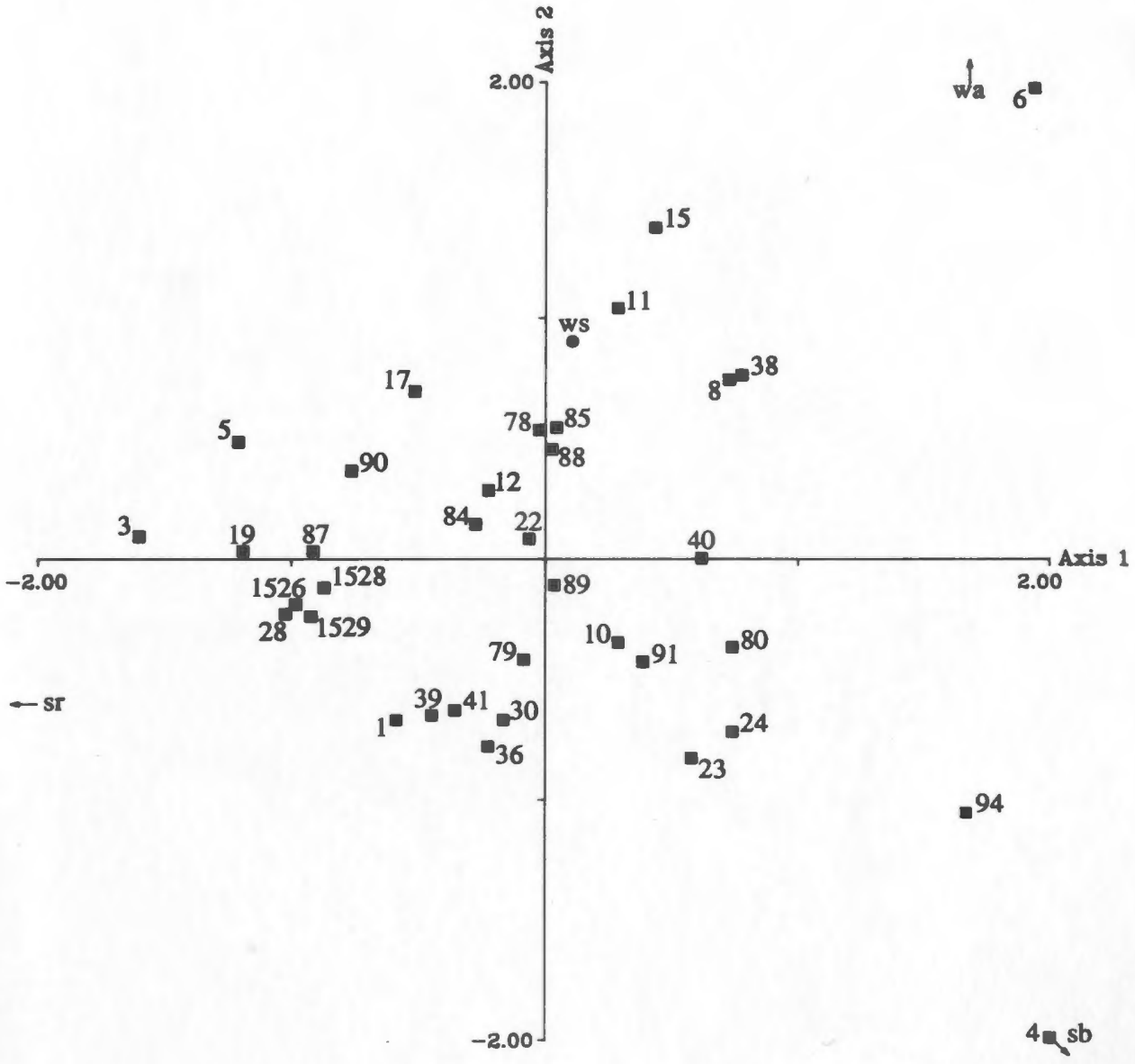

Axis 2
2.00
-2.00
Axis 1
2.00
-2.00
wa
6
15
11
ws
17
38
8
5
78
85
88
90
12
84
22
3
19
87
40
1526
1528
89
28
1529
10
91
80
79
sr
39
41
30
1
24
36
23
94
4
sb

Figure 22. Redundancy Analysis for the **microhabitat** approach, using $\log_e$-transformed percentage data. Sample points (■) are labelled with station numbers (see Table 1), biological variables (●) with lowercase alphanumeric codes (see Figure 2 for explanation of variable codes), and environmental variables (↦) with uppercase labels (abbreviation of variable name). Biological variables situated outside the range of sample points in the ordination are indicated by a small arrow next to the variable code. Scaling factor of environmental biplot scores= 5.8.

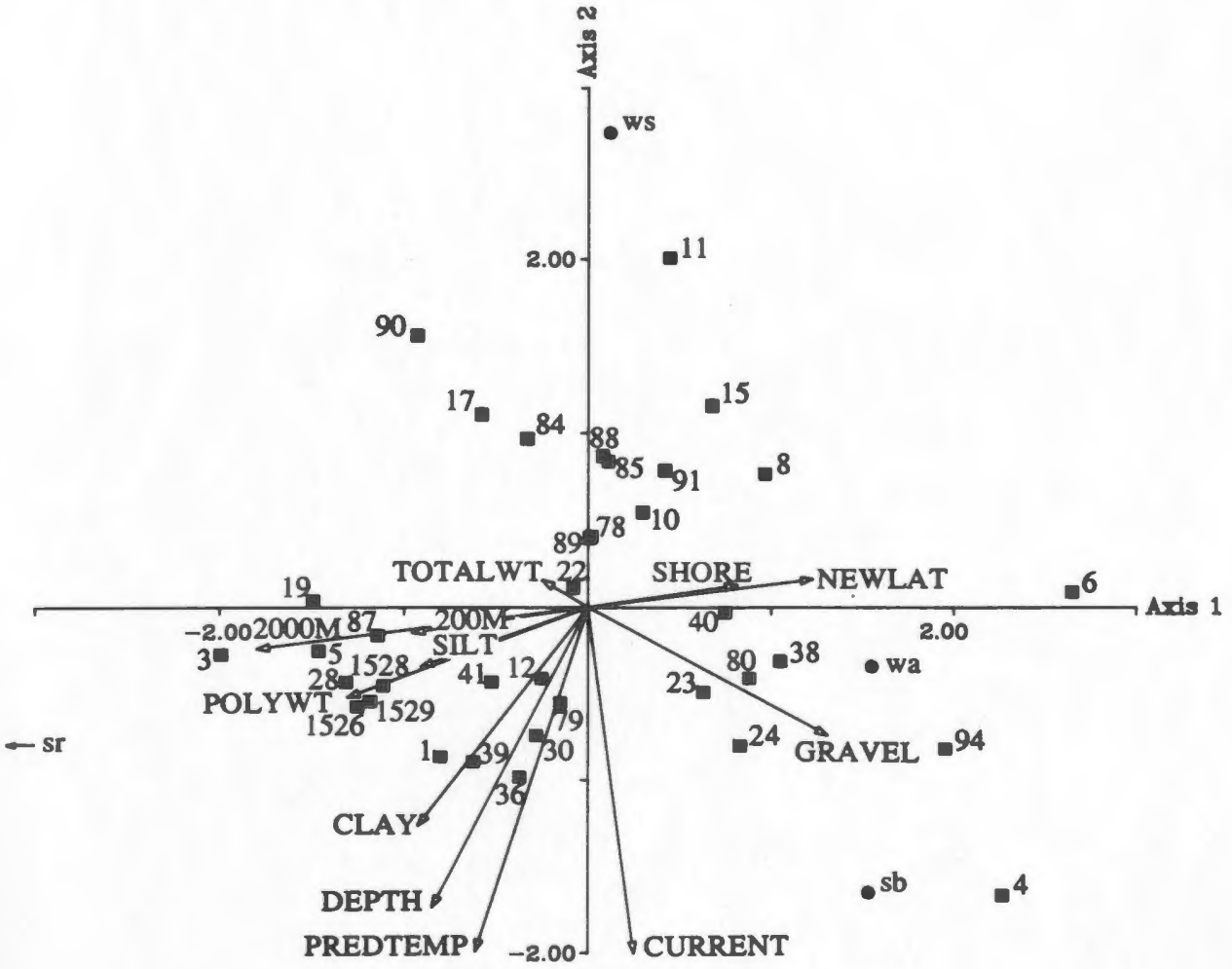

Axis 2
ws
11
2.00
90
17
15
84
88
85
91
8
78
10
89
TOTALWT
22
SHORE
NEWLAT
6
19
Axis 1
-2.00
2000M
87
200M
40
2.00
3
5
SILT
1528
41
12
80
38
wa
28
23
POLYWT
1529
1526
79
sr
1
39
30
24
GRAVEL
94
36
CLAY
sb
4
DEPTH
PREDTEMP
-2.00
CURRENT

Figure 23. Cumulative proportion of variance explained by the first four axes and by all axes (trace) of Principal Components Analysis and Redundancy Analysis for the **microhabitat** approach, using $\log_e$-transformed percentage data.

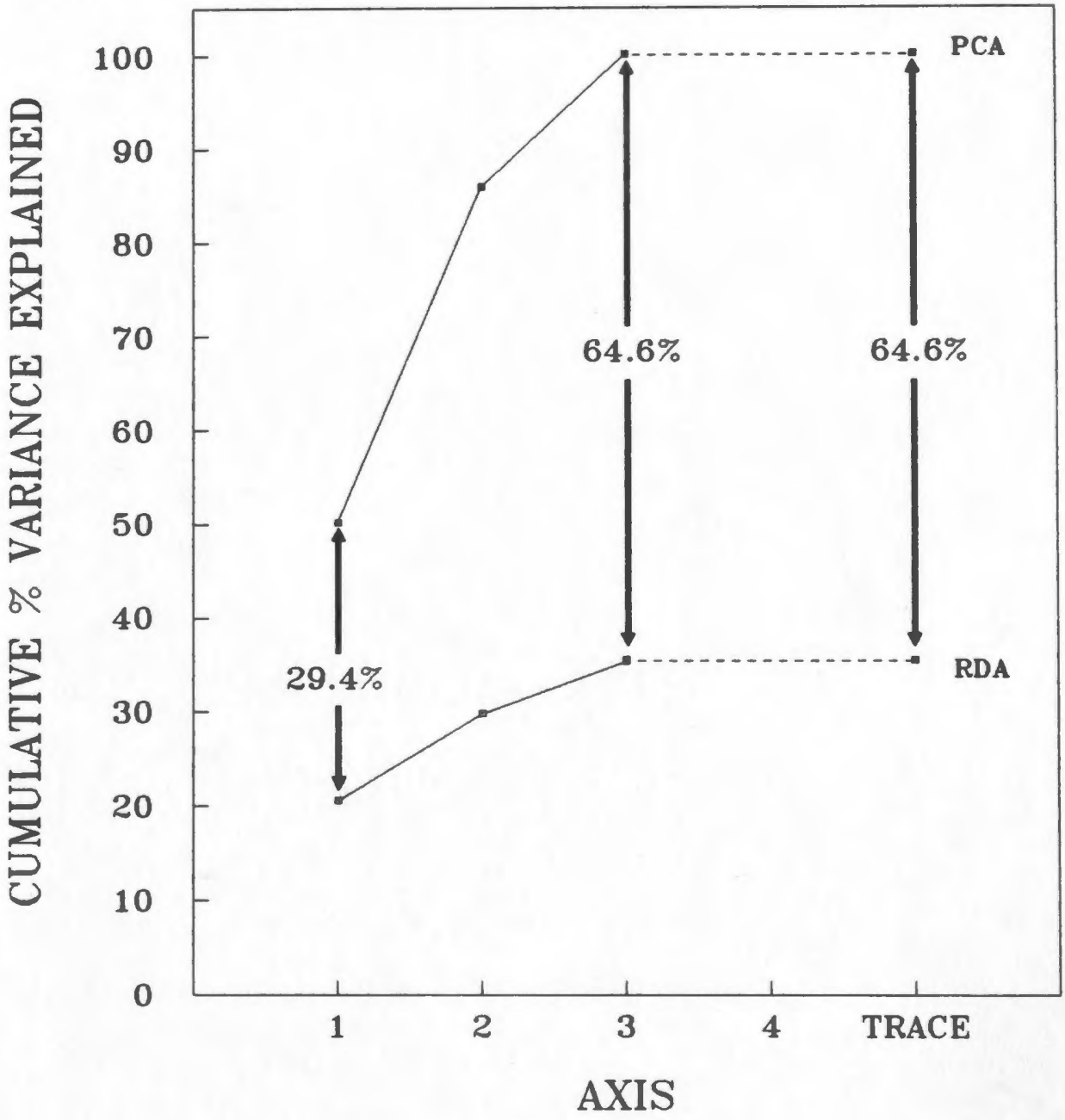

CUMULATIVE % VARIANCE EXPLAINED
100
90
80
70
60
50
40
30
20
10
0
1
2
3
4
TRACE
AXIS
PCA
RDA
64.6%
64.6%
29.4%

Figure 24. Multidimensional scaling ordination of samples based on the **motility pattern** approach, using √√-transformed abundance data (stress value for two dimensions: 0.16). UPGMA groupings are represented by the envelopes around the samples. Data points are labelled with the station number as listed in Table 1.

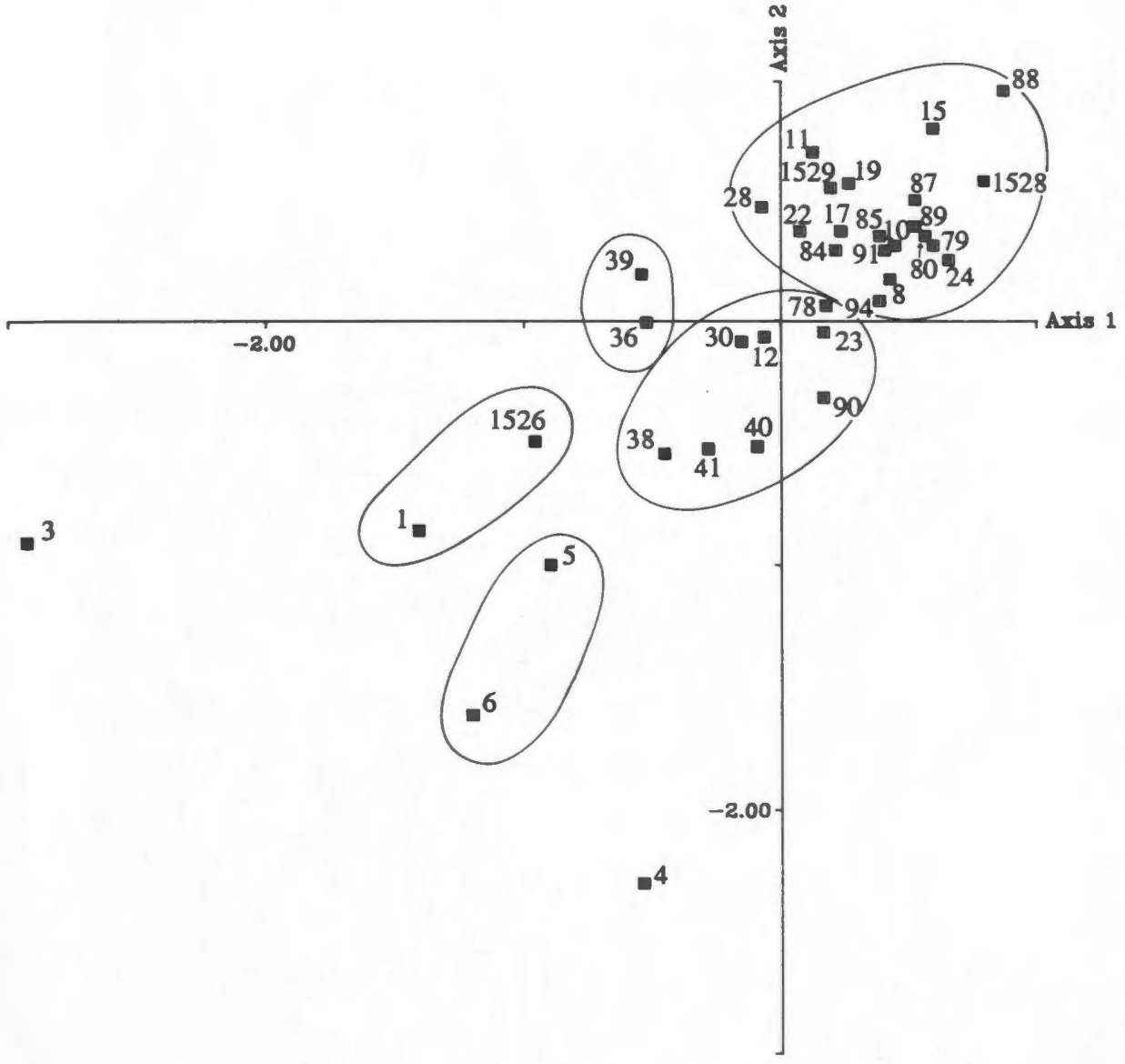

Axis 2
Axis 1
-2.00
-2.00
88
15
11
1529
19
87
1528
28
22
17
85
10
89
84
91
79
80
24
8
39
78
94
36
30
12
23
90
1526
40
38
41
1
3
5
6
4

Figure 25. Principal Components Analysis for the **motility pattern** approach, using √√-transformed abundance data. Sample points (■) are labelled with station numbers (see Table 1) and biological variables (●) with lowercase alphanumeric codes. See Figure 2 for explanation of variable codes. Variables situated outside the range of sample points in the ordination are indicated by a small arrow next to the variable code.

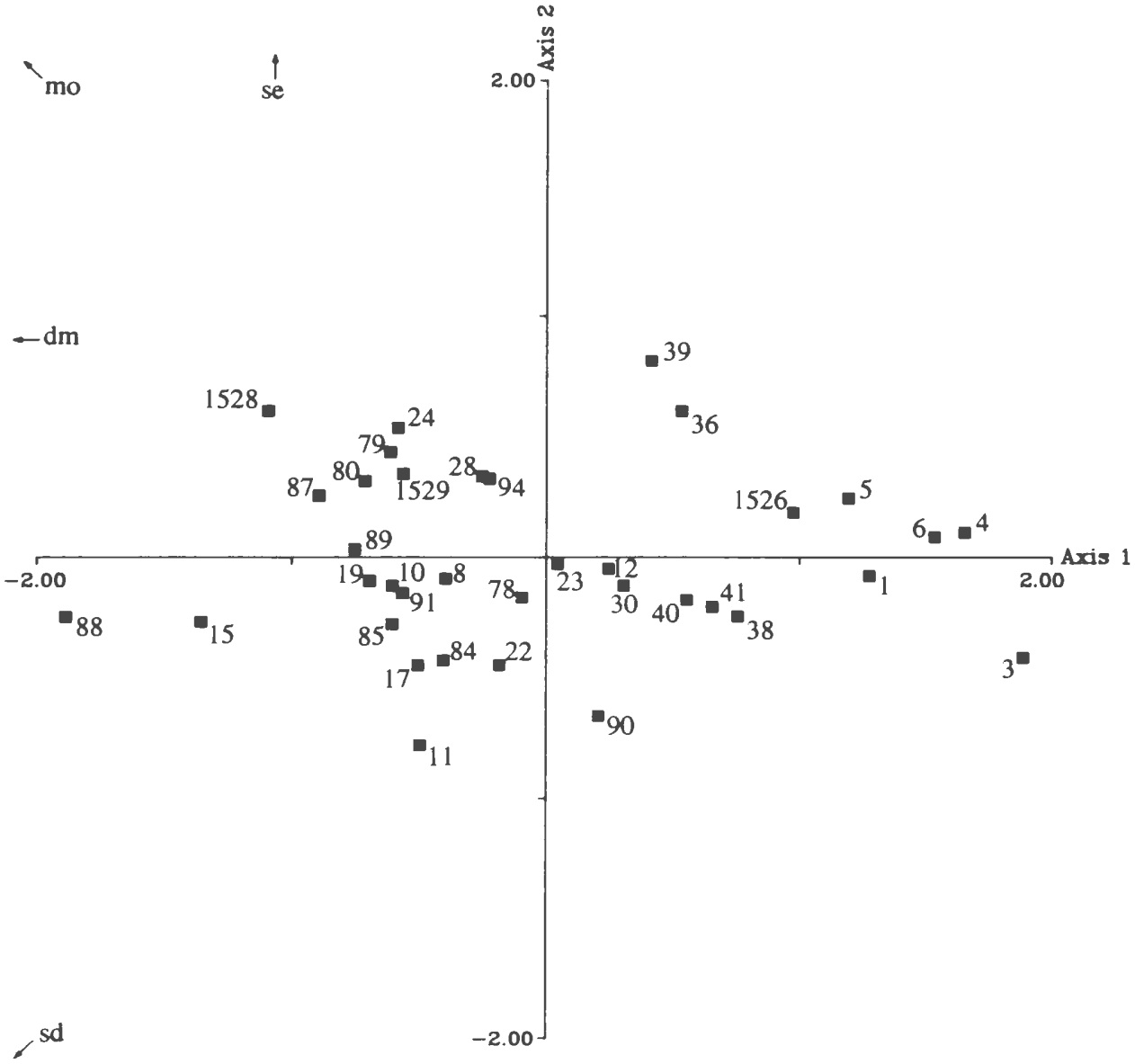

mo
se
dm
sd
Axis 2
Axis 1
2.00
-2.00
-2.00
2.00
1528
24
79
80
87
1529
28
94
89
19
10
8
91
78
88
15
85
84
22
17
11
39
36
1526
5
6
4
23
12
30
40
41
38
1
3
90

Figure 26. Redundancy Analysis for the **motility pattern** approach, using √√-transformed abundance data. Sample points (■) are labelled with station numbers (see Table 1), biological variables (●) with lowercase alphanumeric codes (see Figure 2 for explanation of variable codes), and environmental variables (↦) with uppercase labels (abbreviation of variable name). Biological variables situated outside the range of sample points in the ordination are indicated by a small arrow next to the variable code. Scaling factor of environmental biplot scores= 3.87.

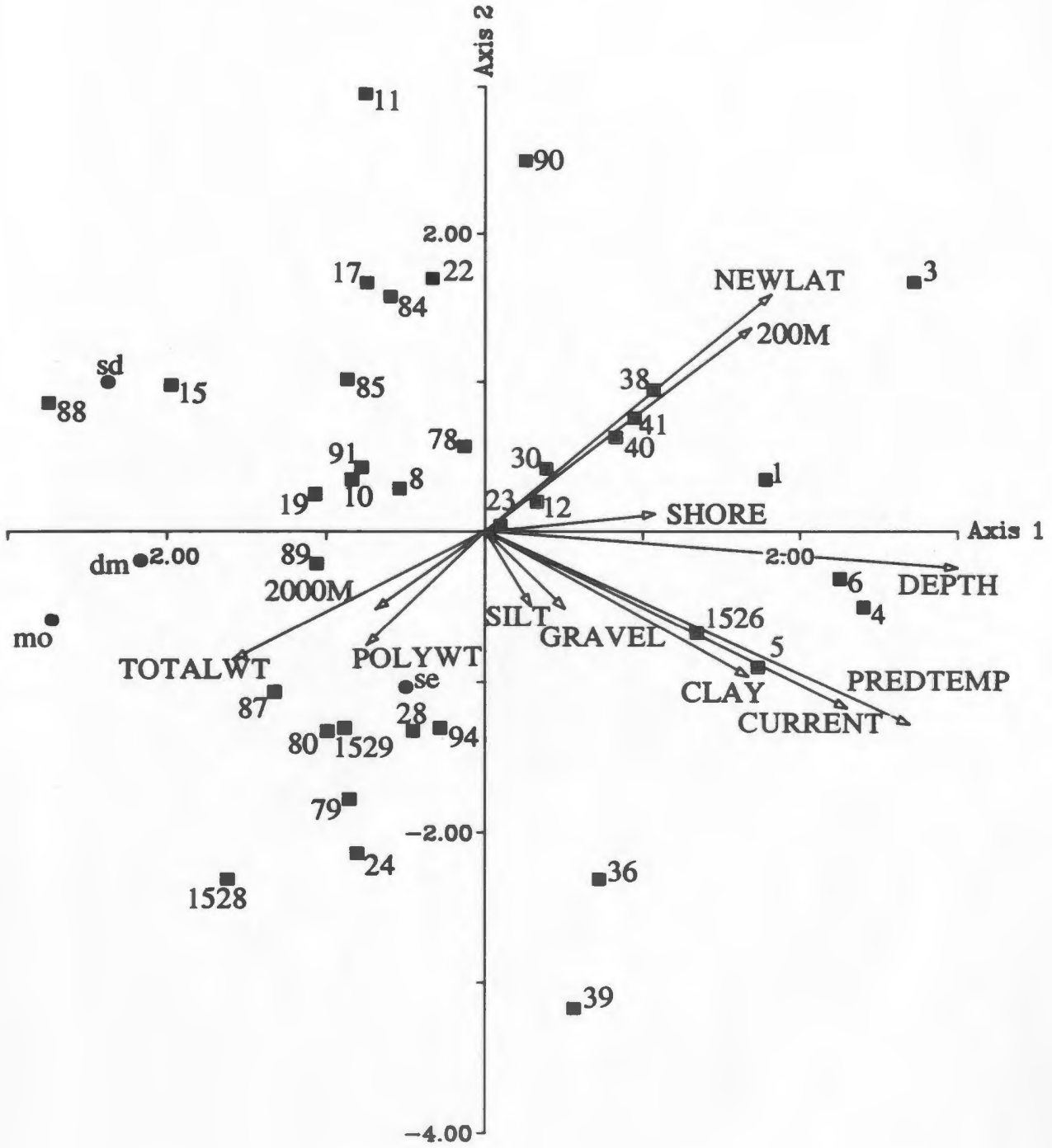

Axis 2
Axis 1
11
90
2.00
17
22
84
NEWLAT
3
200M
sd
15
88
85
38
41
40
78
91
30
1
8
19
10
23
12
SHORE
dm
2.00
89
2000M
2:00
6
DEPTH
4
mo
SILT
GRAVEL
1526
5
TOTALWT
POLYWT
se
CLAY
PREDTEMP
87
28
CURRENT
80
1529
94
79
-2.00
24
36
1528
39
-4.00

Figure 27. Cumulative proportion of variance explained by the first four axes and by all axes (trace) of Principal Components Analysis and Redundancy Analysis for the **motility pattern** approach, using √√-transformed abundance data.

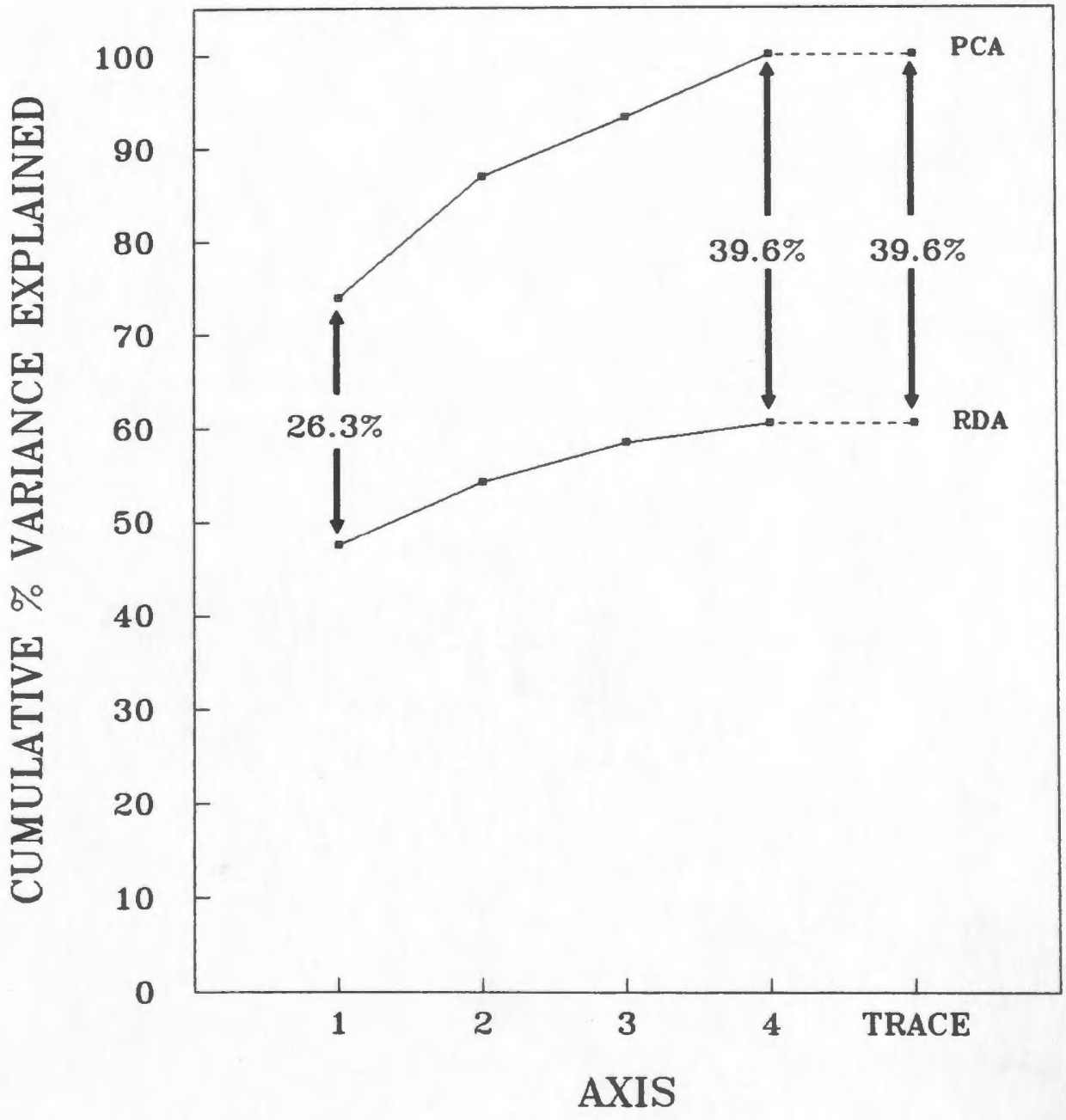

CUMULATIVE % VARIANCE EXPLAINED
100
90
80
70
60
50
40
30
20
10
0
1
2
3
4
TRACE
AXIS
PCA
RDA
26.3%
39.6%
39.6%

Figure 28. Multidimensional scaling ordination of samples based on the **motility pattern** approach, using arcsin$\sqrt{\cdot}$-transformed percentage data (stress value for two dimensions: 0.21). UPGMA groupings are represented by the envelopes around the samples. Data points are labelled with the station number as listed in Table 1.

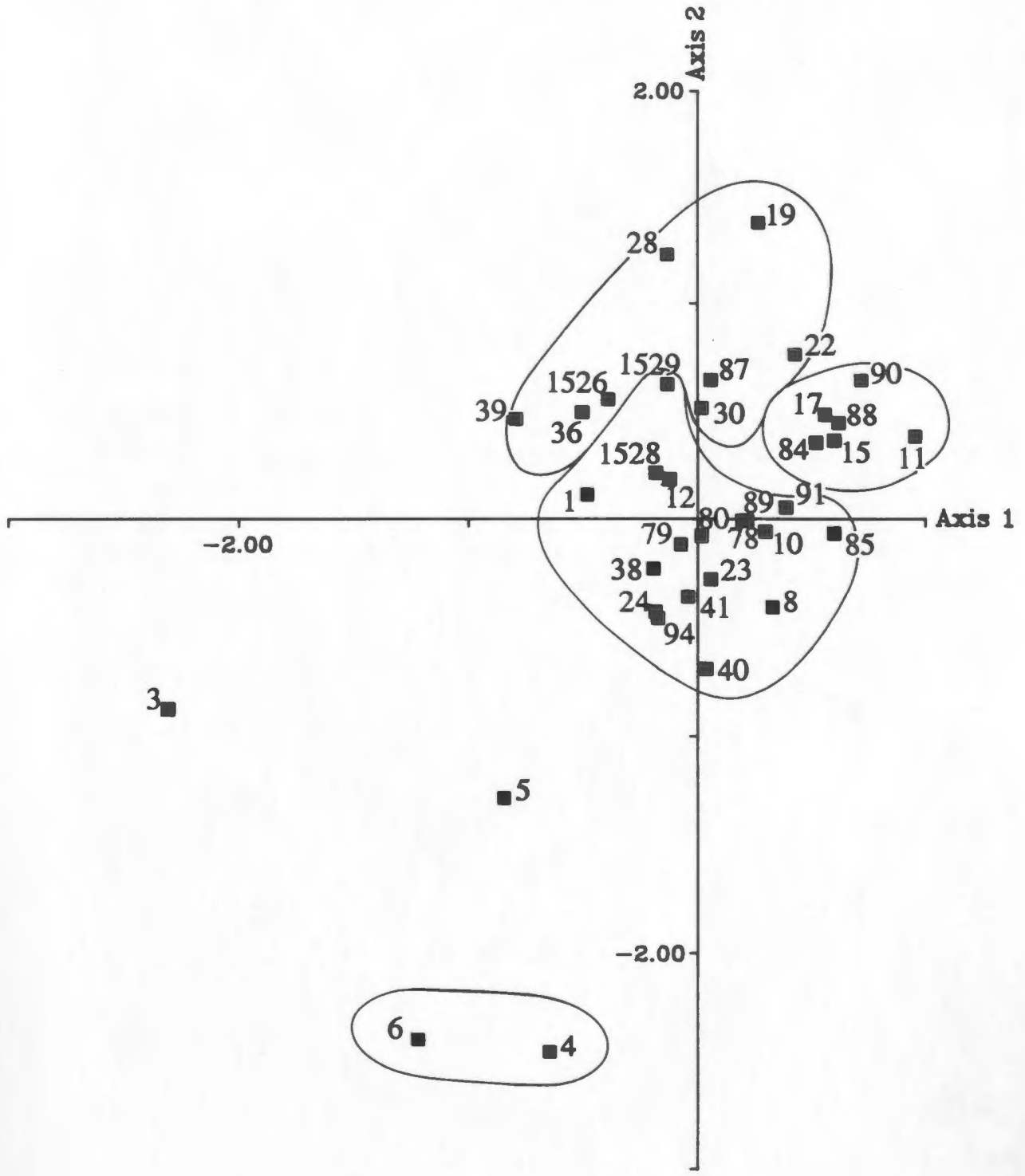

Axis 2
2.00
-2.00
Axis 1
-2.00
19
28
22
1529
87
90
1526
17
88
39
30
36
84
15
11
1528
1
12
89
91
80
79
78
10
85
38
23
24
41
8
94
40
3
5
6
4

Figure 29. Principal Components Analysis for the **motility pattern** approach, using $\log_e$-transformed percentage data. Sample points (■) are labelled with station numbers (see Table 1) and biological variables (●) with lowercase alphanumeric codes. See Figure 2 for explanation of variable codes. Variables situated outside the range of sample points in the ordination are indicated by a small arrow next to the variable code.

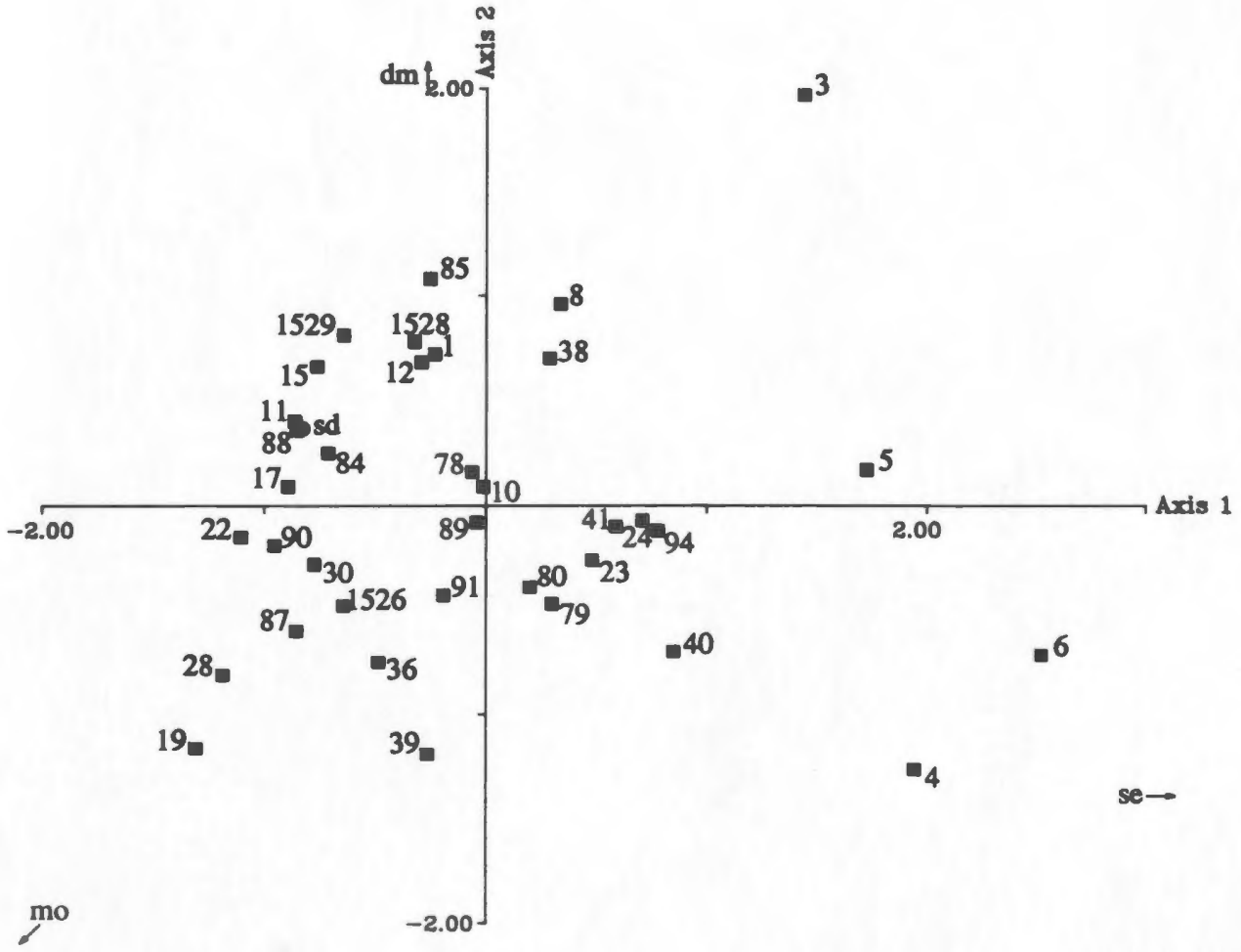

Axis 2
dm
2.00
3
85
8
1529
1528
1
38
15
12
11
sd
88
84
78
5
17
10
Axis 1
-2.00
22
90
89
41
24
94
2.00
30
80
23
1526
91
79
87
40
6
28
36
19
39
4
se
mo
-2.00

Figure 30. Redundancy Analysis for the **motility pattern** approach, using $\log_e$-transformed percentage data. Sample points (■) are labelled with station numbers (see Table 1), biological variables (●) with lowercase alphanumeric codes (see Figure 2 for explanation of variable codes), and environmental variables (→) with uppercase labels (abbreviation of variable name). Biological variables situated outside the range of sample points in the ordination are indicated by a small arrow next to the variable code. Scaling factor of environmental biplot scores= 6.65.

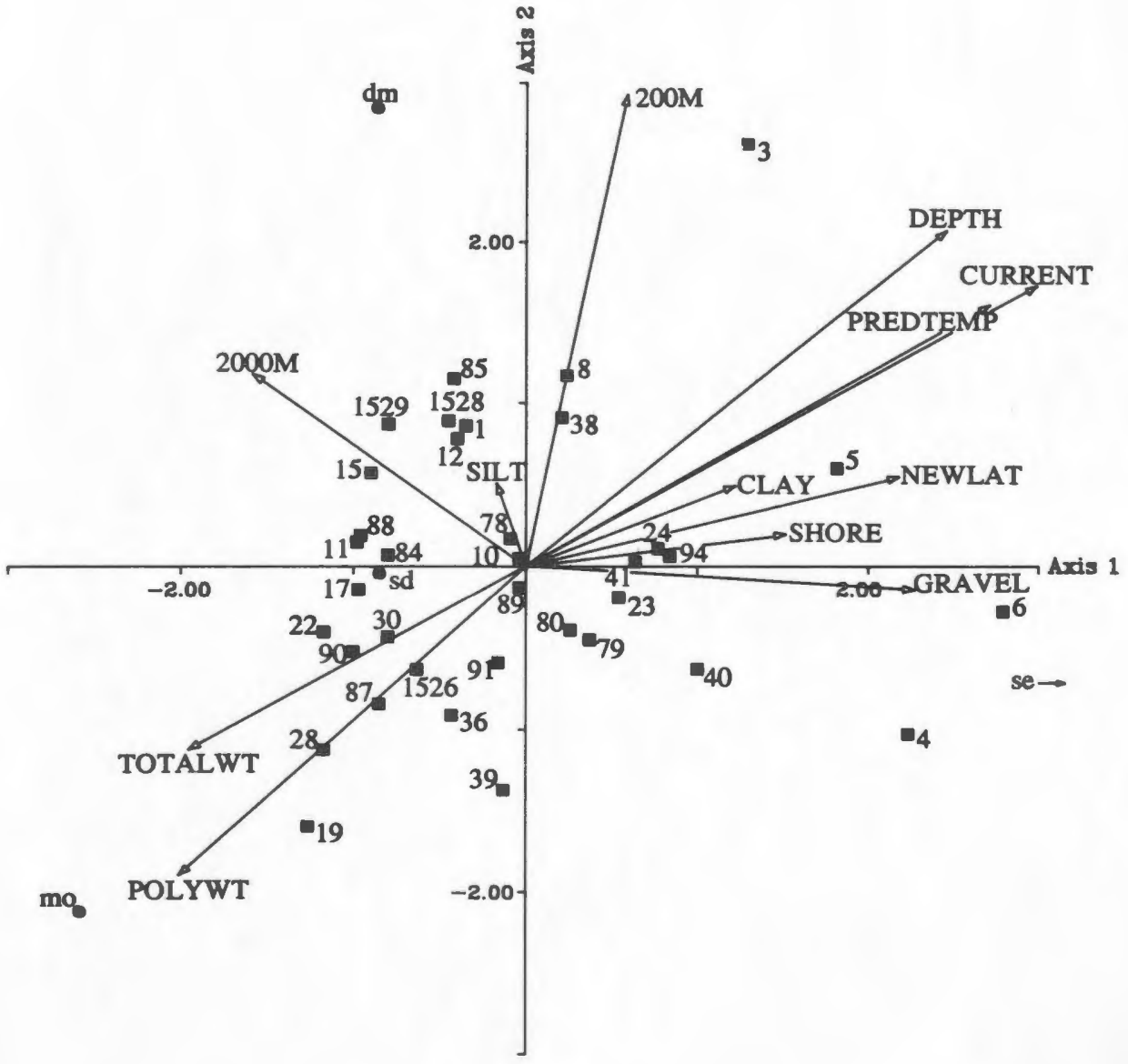

Axis 2
Axis 1
dm
200M
3
DEPTH
CURRENT
PREDTEMP
2.00
2000M
85
8
1529
1528
1
38
12
15
SILT
5
CLAY
NEWLAT
88
78
24
SHORE
11
84
10
94
sd
41
GRAVEL
-2.00
17
89
23
6
22
30
80
79
90
91
40
se
87
1526
36
4
28
TOTALWT
39
19
mo
POLYWT
-2.00

Figure 31. Cumulative proportion of variance explained by the first four axes and by all axes (trace) of Principal Components Analysis and Redundancy Analysis for the **motility pattern** approach, using $\log_e$-transformed percentage data.

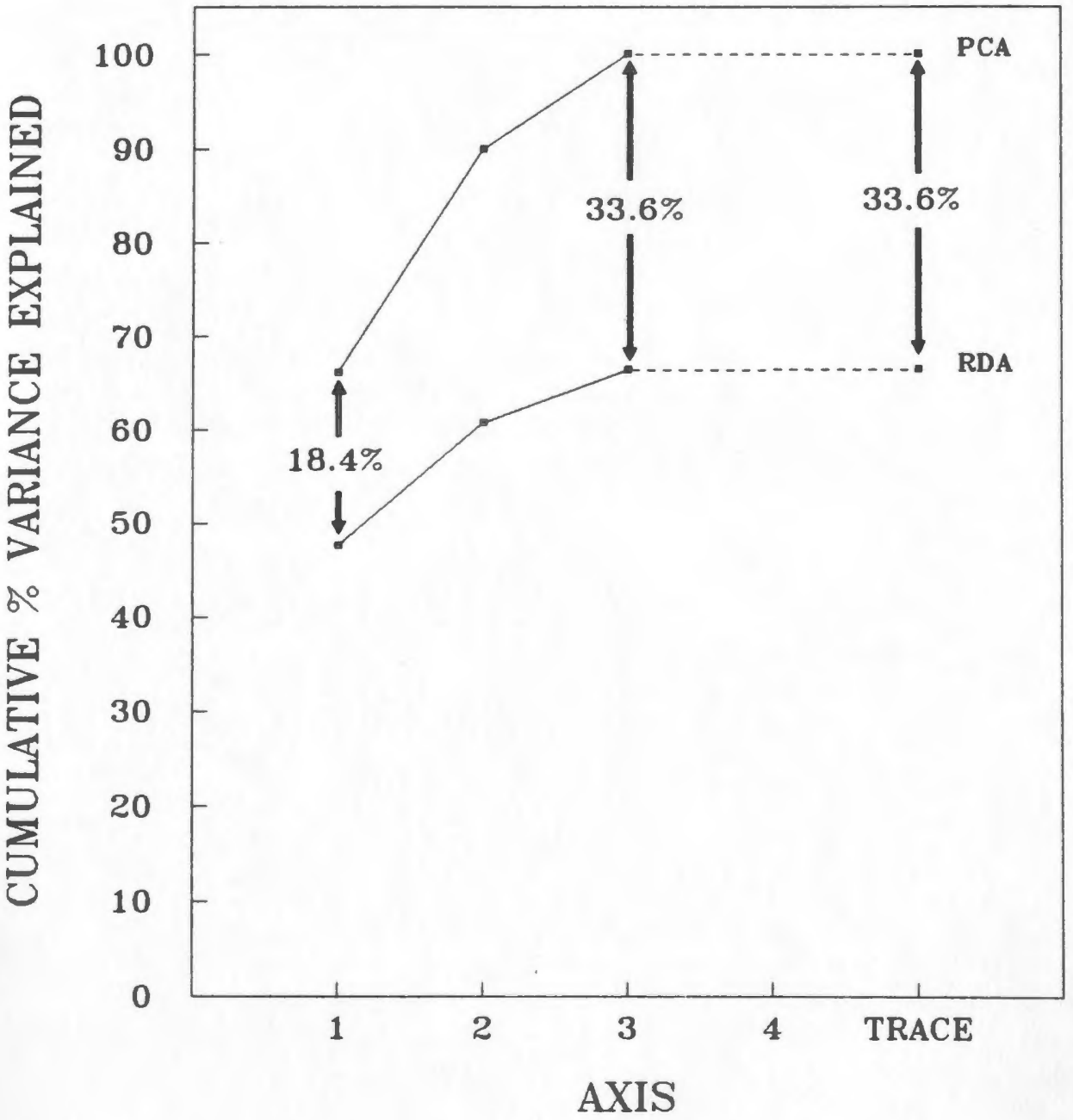

CUMULATIVE % VARIANCE EXPLAINED
100
90
80
70
60
50
40
30
20
10
0
PCA
RDA
33.6%
33.6%
18.4%
1
2
3
4
TRACE
AXIS

Figure 32. Multidimensional scaling ordination of samples based on the **body size** approach, using √√-transformed abundance data (stress value for two dimensions: 0.15). UPGMA groupings are represented by the envelopes around the samples. Data points are labelled with the station number as listed in Table 1.

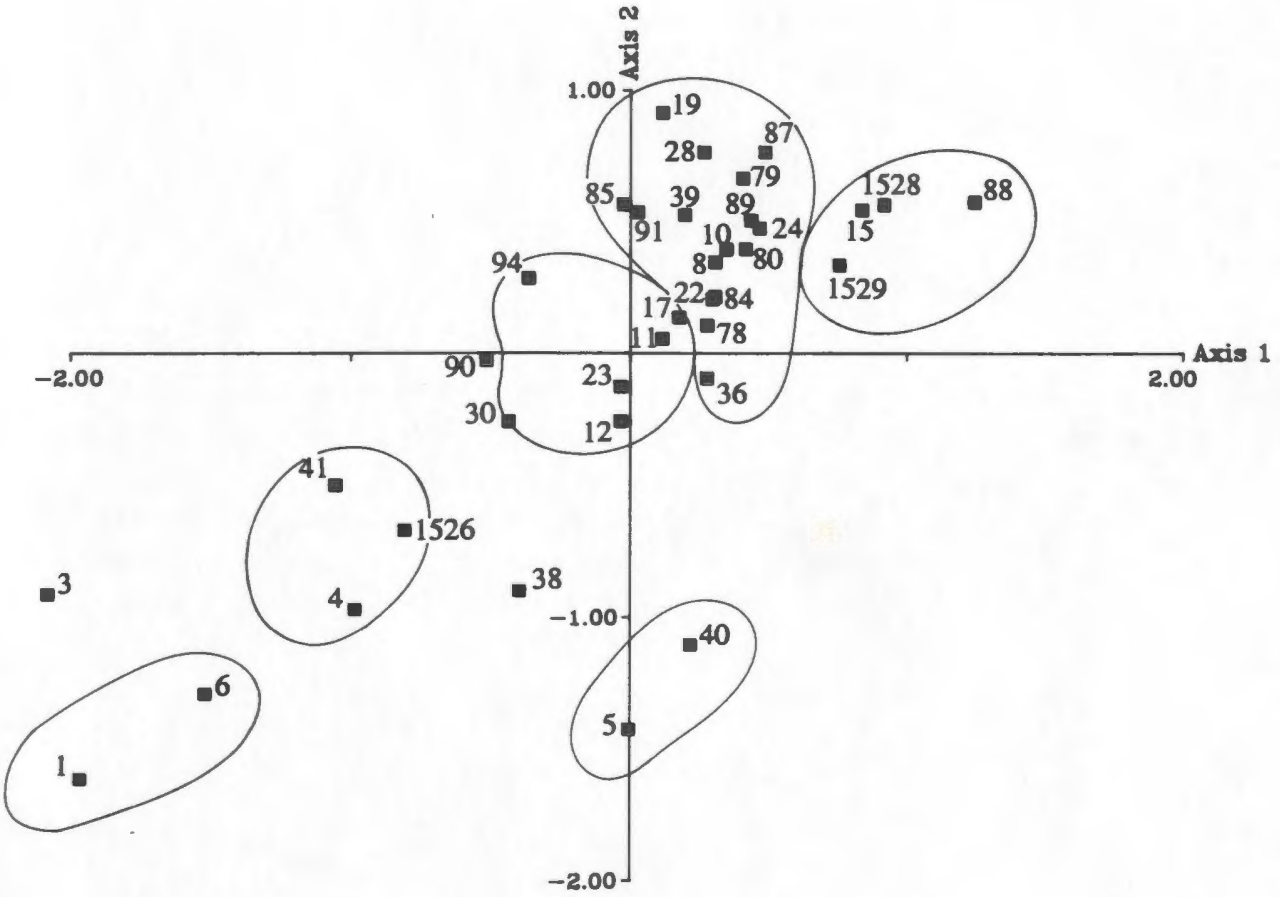

Axis 2
1.00
19
87
28
79
85
39
89
1528
88
91
10
24
15
94
8
80
1529
22
84
17
78
11
Axis 1
−2.00
90
23
2.00
36
30
12
41
1526
3
38
4
−1.00
40
6
5
1
−2.00

Figure 33. Principal Components Analysis for the **body size** approach, using √√-transformed abundance data. Sample points (■) are labelled with station numbers (see Table 1) and biological variables (●) with lowercase alphanumeric codes. See Figure 2 for explanation of variable codes. Variables situated outside the range of sample points in the ordination are indicated by a small arrow next to the variable code.

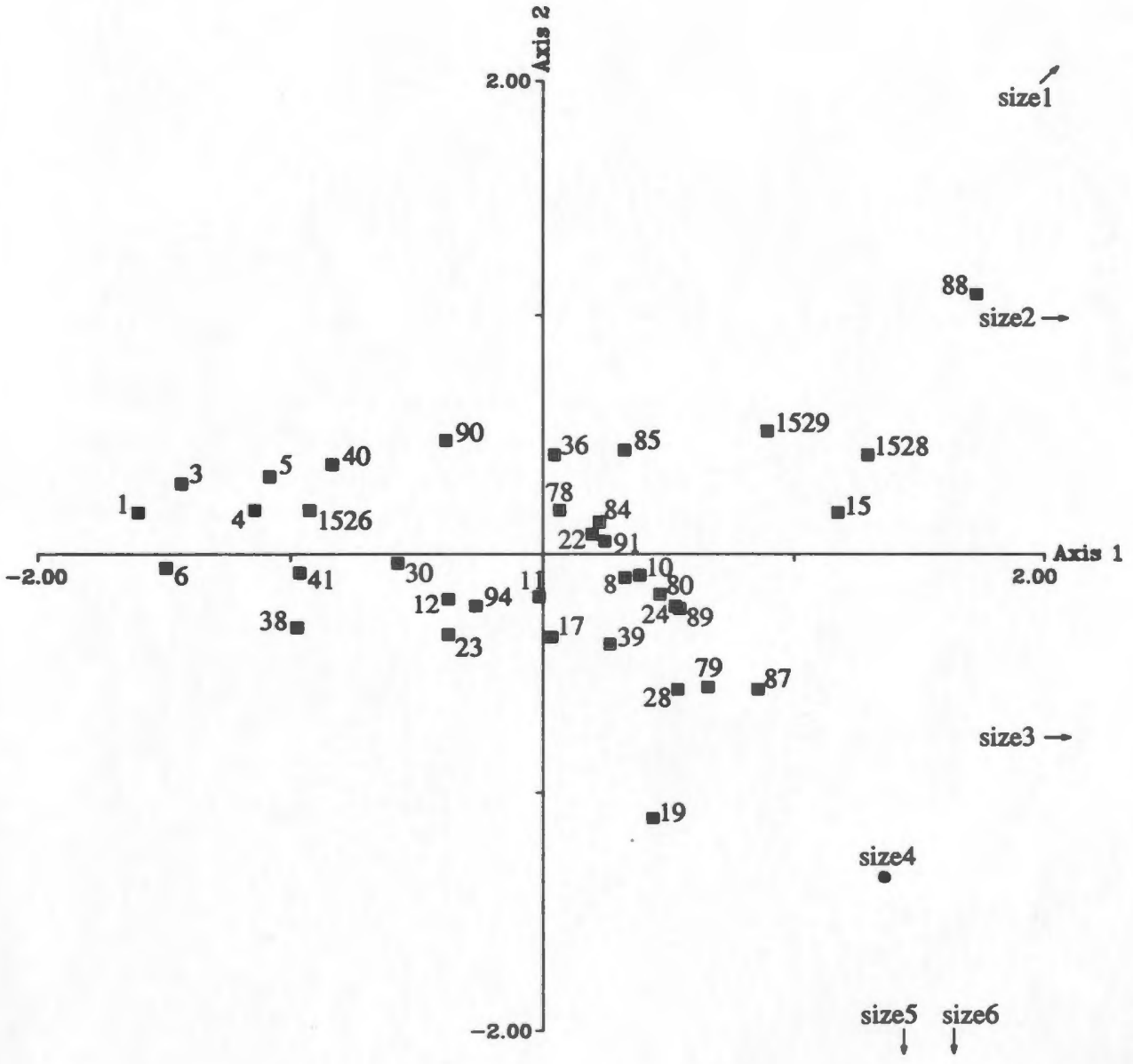

Axis 2
2.00
-2.00
Axis 1
-2.00
2.00
size1
88
size2
1529
90
36
85
1528
40
5
3
78
84
15
1
4
1526
22
91
6
41
30
11
8
10
80
12
94
24
89
38
17
39
23
79
87
28
size3
19
size4
size5
size6

Figure 34. Redundancy Analysis for the **body size** approach, using √√-transformed abundance data. Sample points (■) are labelled with station numbers (see Table 1), biological variables (●) with lowercase alphanumeric codes (see Figure 2 for explanation of variable codes), and environmental variables (↦) with uppercase labels (abbreviation of variable name). Biological variables situated outside the range of sample points in the ordination are indicated by a small arrow next to the variable code. Scaling factor of environmental biplot scores= 3.3.

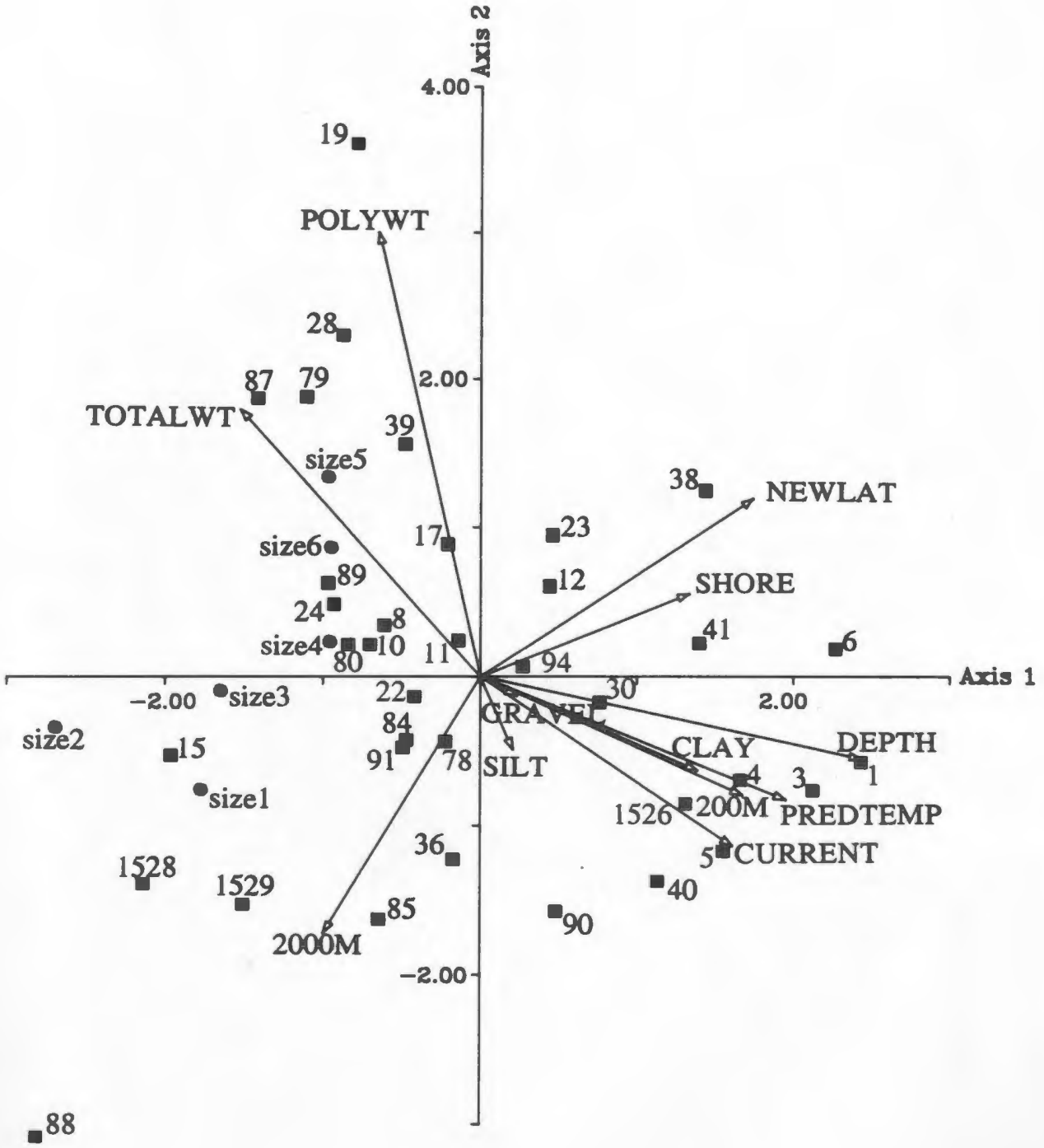

Axis 2
4.00
2.00
-2.00
Axis 1
-2.00
2.00
19
POLYWT
28
87
79
TOTALWT
39
size5
38
NEWLAT
23
17
size6
89
12
SHORE
24
8
41
6
size4
80
10
11
94
22
30
size3
GRAVEL
84
size2
15
91
78
SILT
CLAY
DEPTH
4
3
1
size1
1526
200M
PREDTEMP
36
5
CURRENT
1528
1529
40
85
90
2000M
88

Figure 35. Cumulative proportion of variance explained by the first four axes and by all axes (trace) of Principal Components Analysis and Redundancy Analysis for the **body size** approach, using √√-transformed abundance data.

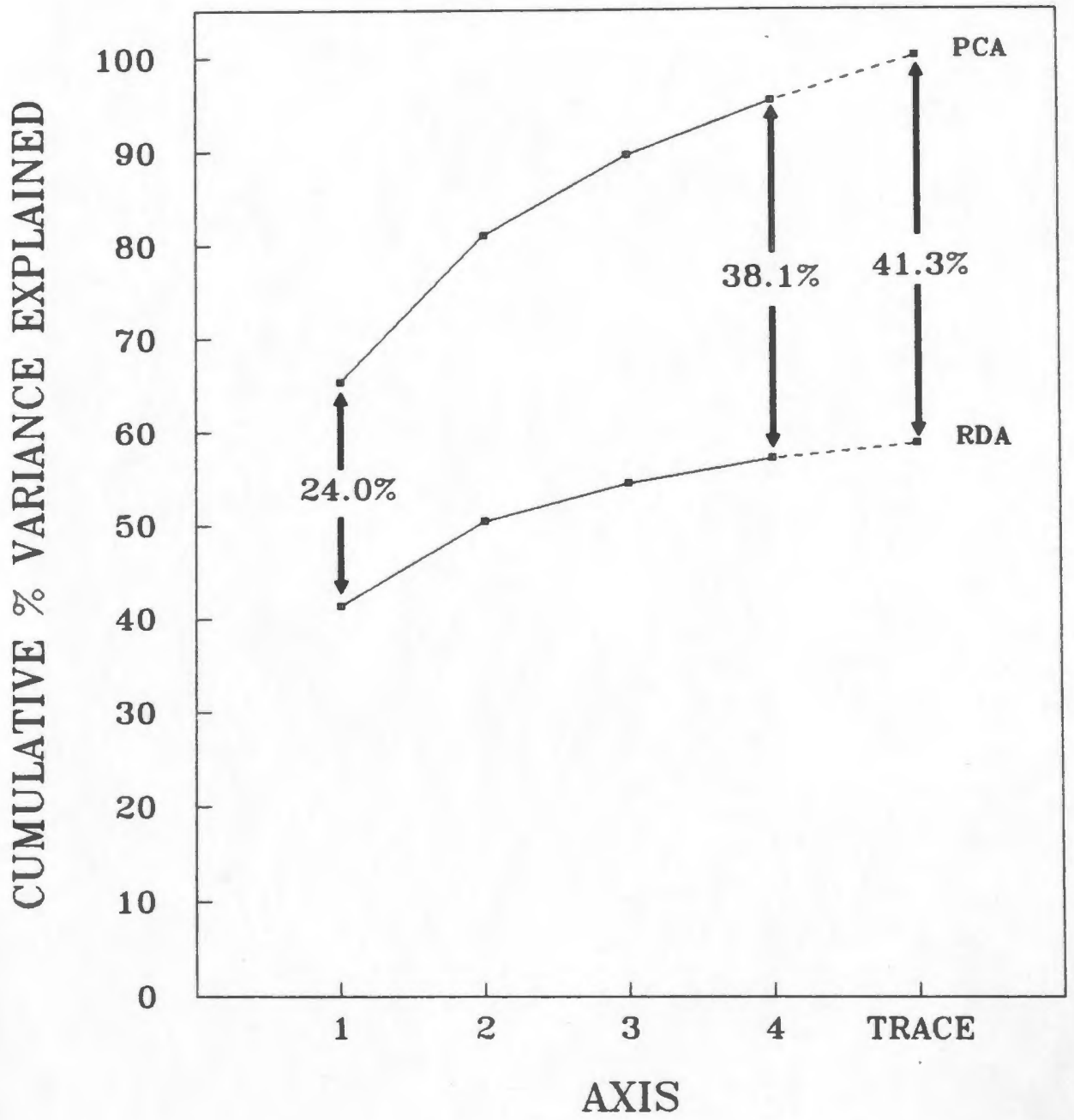

CUMULATIVE % VARIANCE EXPLAINED
100
90
80
70
60
50
40
30
20
10
0
PCA
RDA
24.0%
38.1%
41.3%
1
2
3
4
TRACE
AXIS

Figure 36. Multidimensional scaling ordination of samples based on the **body size** approach, using arcsin$\sqrt{}$-transformed percentage data (stress value for two dimensions: 0.27). UPGMA groupings are represented by the envelopes around the samples. Data points are labelled with the station number as listed in Table 1.

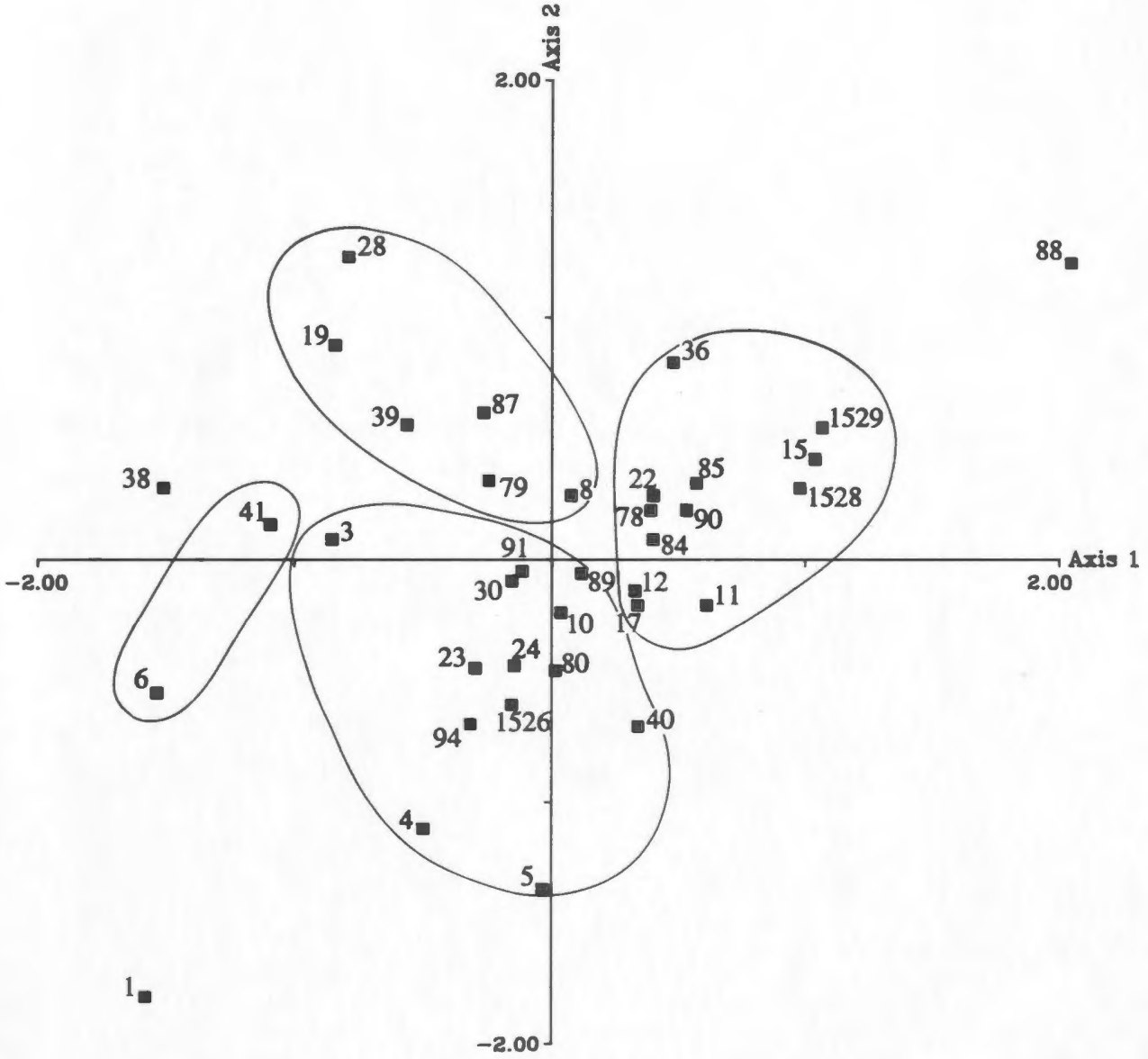

Axis 2
2.00
-2.00
Axis 1
-2.00
2.00
28
88
19
36
39
87
1529
15
38
79
8
22
85
1528
41
78
90
3
84
91
89
12
30
11
10
17
23
24
80
6
94
1526
40
4
5
1

Figure 37. Principal Components Analysis for the **body size** approach, using $\log_e$-transformed percentage data. Sample points (■) are labelled with station numbers (see Table 1) and biological variables (●) with lowercase alphanumeric codes. See Figure 2 for explanation of variable codes. Variables situated outside the range of sample points in the ordination are indicated by a small arrow next to the variable code.

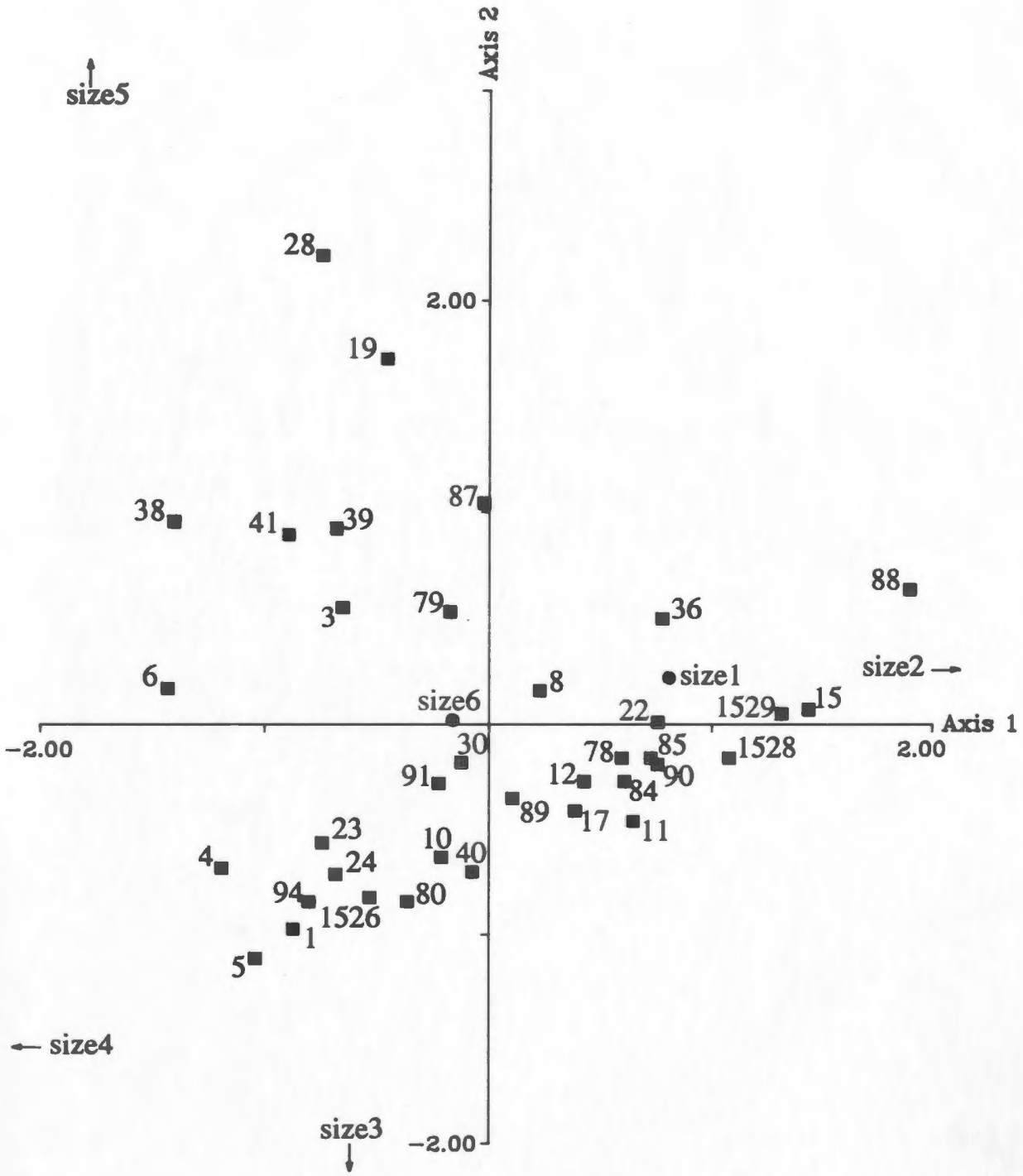

Axis 2
size5
28
2.00
19
87
38
41
39
88
3
79
36
6
8
size1
size2
size6
22
1529
15
Axis 1
-2.00
30
78
85
1528
2.00
91
12
90
84
89
17
11
23
10
40
4
24
94
80
1526
1
5
size4
size3
-2.00

Figure 38. Redundancy Analysis for the **body size** approach, using $\log_e$-transformed percentage data. Sample points (■) are labelled with station numbers (see Table 1), biological variables (●) with lowercase alphanumeric codes (see Figure 2 for explanation of variable codes), and environmental variables (↦) with uppercase labels (abbreviation of variable name). Biological variables situated outside the range of sample points in the ordination are indicated by a small arrow next to the variable code. Scaling factor of environmental biplot scores= 6.08.

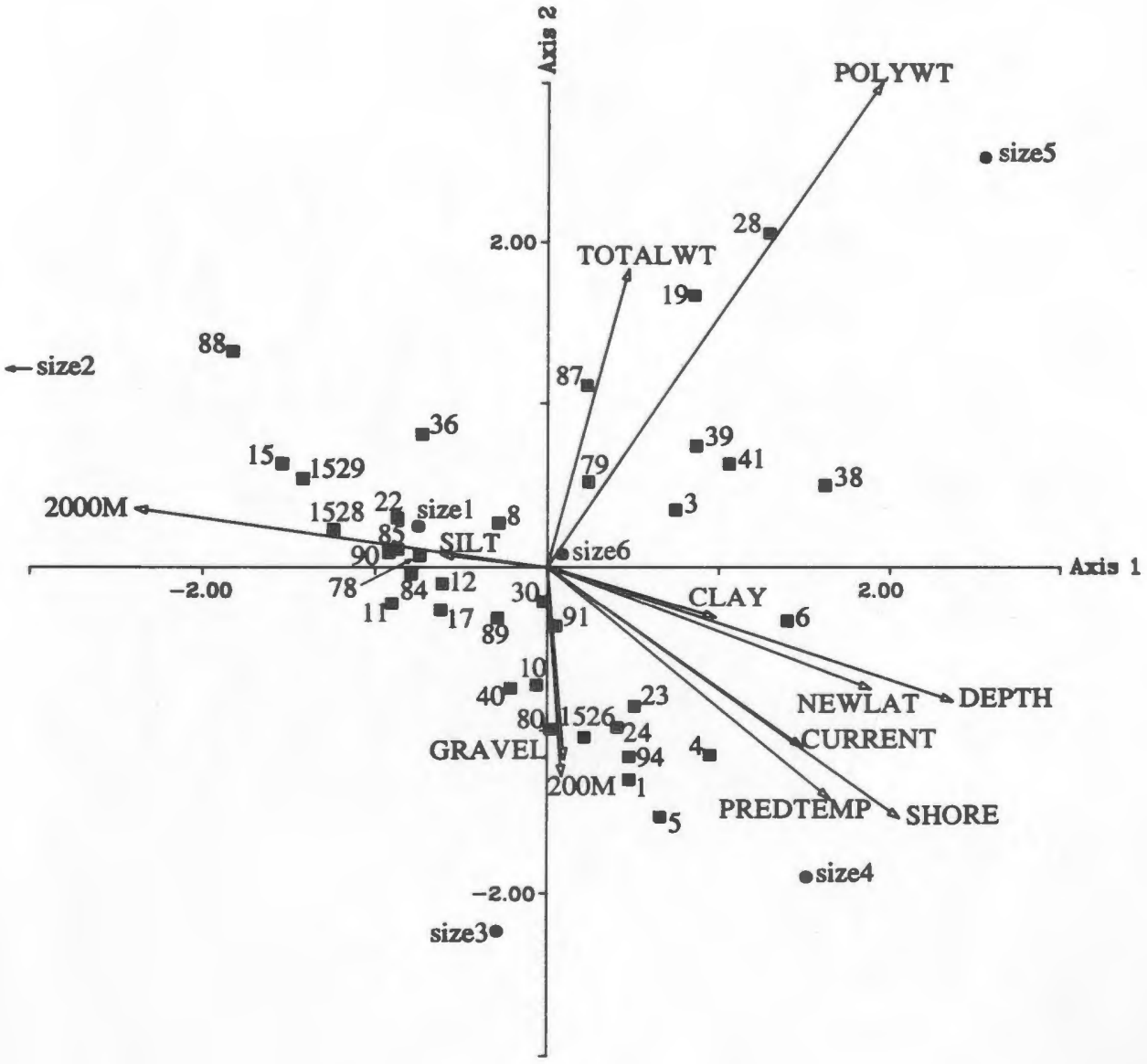

Axis 2
POLYWT
size5
28
2.00
TOTALWT
19
88
size2
87
36
39
41
15
1529
79
38
2000M
1528
22
size1
8
3
85
SILT
90
size6
Axis 1
-2.00
78
84
12
30
CLAY
2.00
11
17
91
6
89
10
40
23
NEWLAT
DEPTH
80
1526
24
CURRENT
GRAVEL
94
4
200M
1
PREDTEMP
SHORE
5
size4
-2.00
size3

Figure 39. Cumulative proportion of variance explained by the first four axes and by all axes (trace) of Principal Components Analysis and Redundancy Analysis for the **body size** approach, using $\log_e$-transformed percentage data.

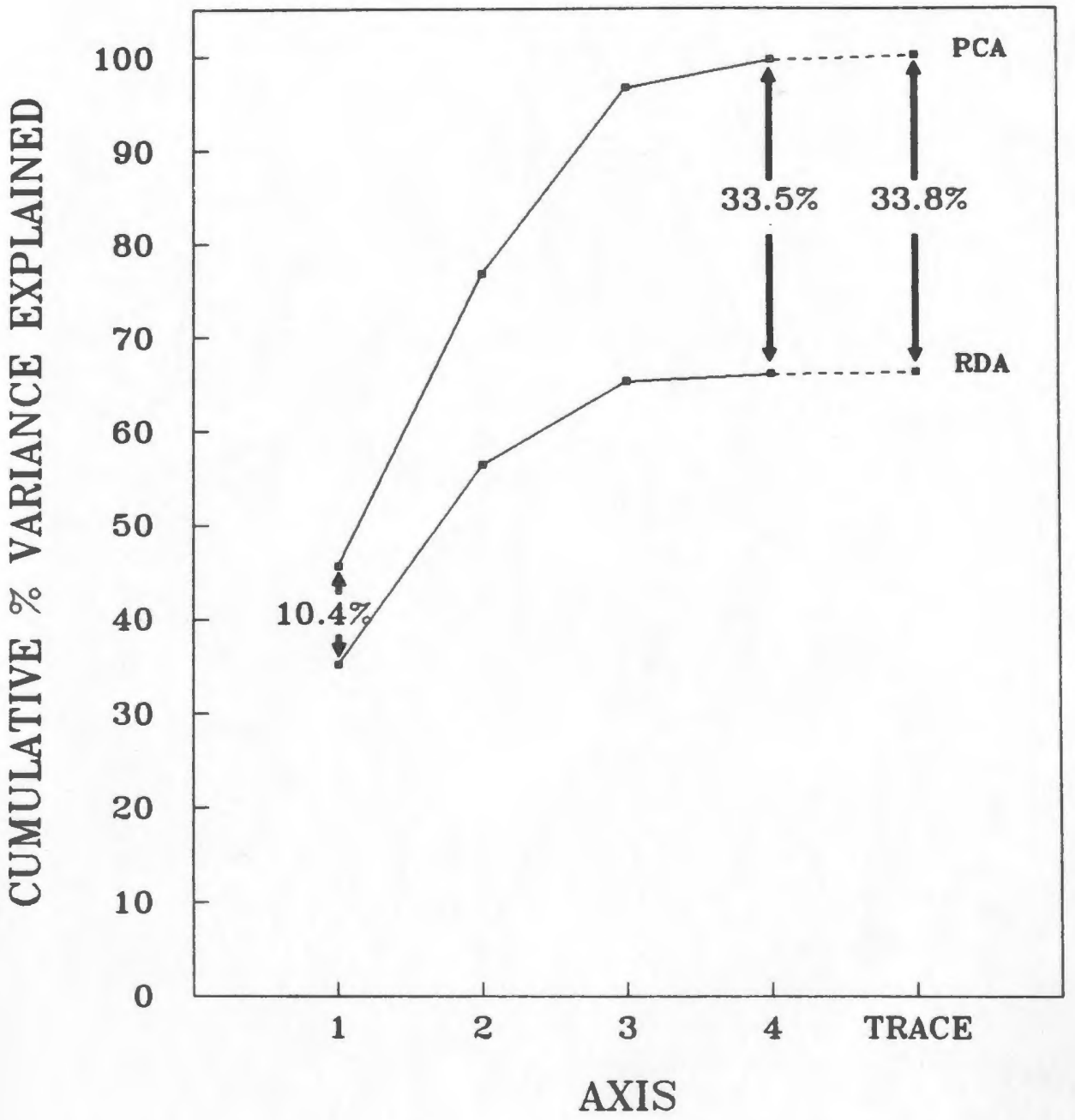

CUMULATIVE % VARIANCE EXPLAINED
100
90
80
70
60
50
40
30
20
10
0
PCA
RDA
33.5%
33.8%
10.4%
1
2
3
4
TRACE
AXIS

Figure 40. Multidimensional scaling ordination of samples based on the **foraging mode/body size** approach, using $\sqrt{\sqrt{}}$-transformed abundance data (stress value for two dimensions: 0.21). UPGMA groupings are represented by the envelopes around the samples. Data points are labelled with the station number as listed in Table 1.

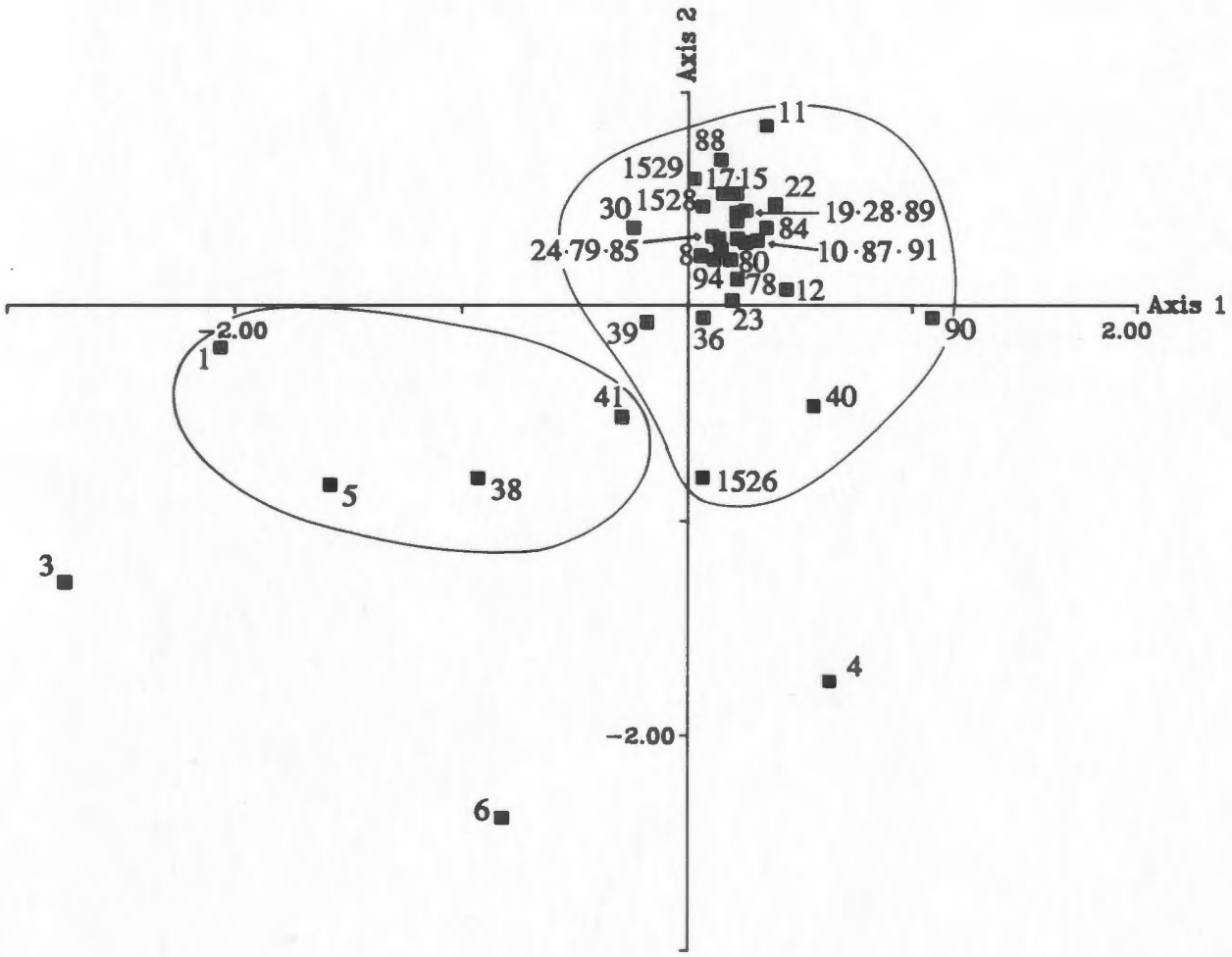

Axis 2
Axis 1
2.00
-2.00
11
88
1529
17·15
22
30
1528
19·28·89
84
24·79·85
10·87·91
80
94
78
12
23
39
36
90
1
41
40
5
38
1526
3
4
6

Figure 41. Principal Components Analysis for the **foraging mode/body size** approach, using √√-transformed abundance data. Sample points (■) are labelled with station numbers (see Table 1) and biological variables (●) with lowercase alphanumeric codes. See Figure 2 for explanation of variable codes. Variables situated outside the range of sample points in the ordination are indicated by a small arrow next to the variable code.

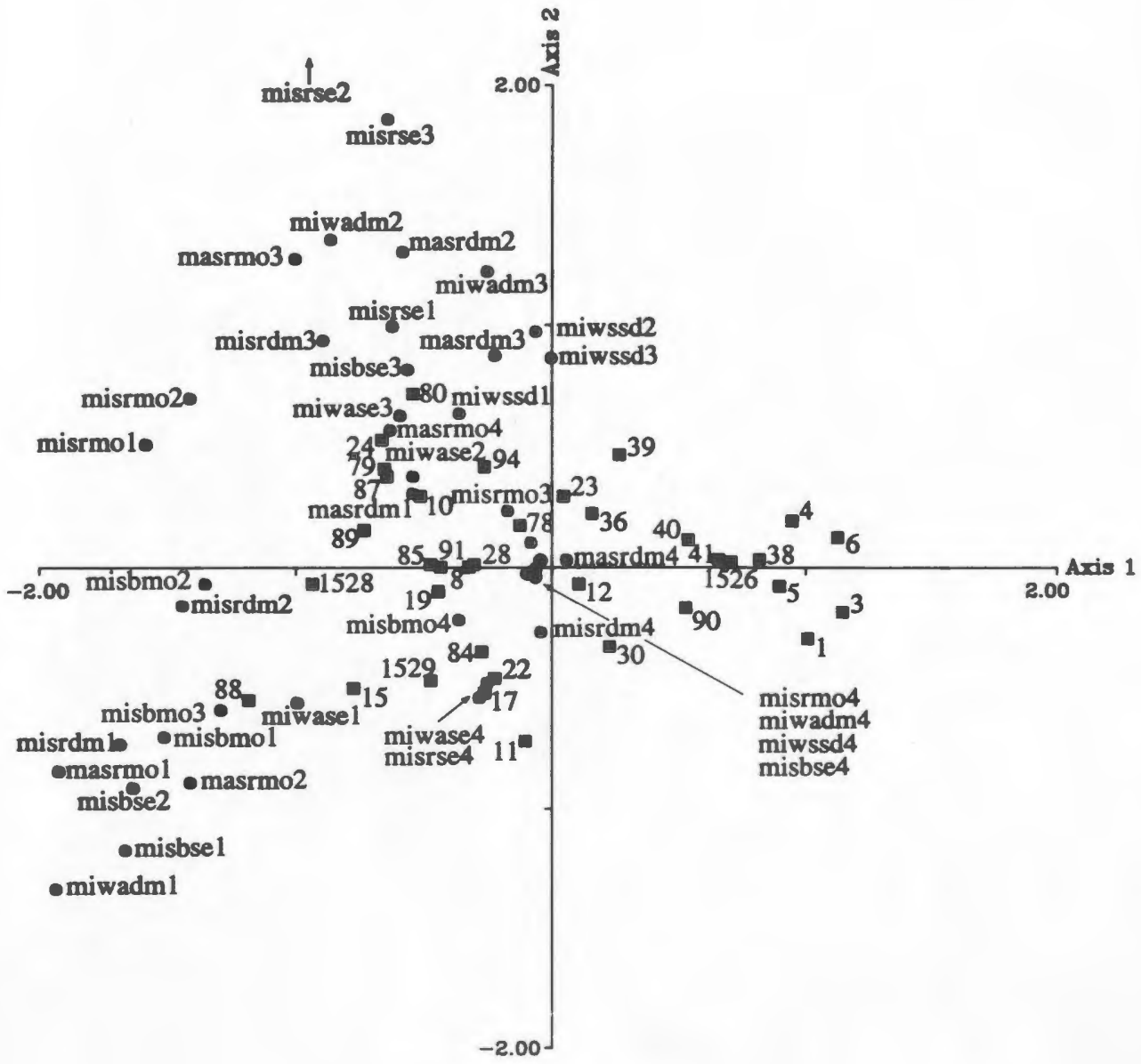

Axis 2
2.00
-2.00
Axis 1
-2.00
2.00
misrse2
misrse3
miwadm2
masrdm2
masrmo3
miwadm3
misrse1
misrdm3
masrdm3
miwssd2
miwssd3
misbse3
misrmo2
80
miwssd1
miwase3
masrmo4
misrmo1
24
miwase2
94
39
79
87
masrdm1
10
misrmo3
23
4
89
78
36
40
6
85
91
28
masrdm4
41
38
misbmo2
1528
8
1526
5
misrdm2
19
12
3
misbmo4
misrdm4
90
84
30
1
1529
22
88
15
17
misbmo3
miwase1
misrdm1
misbmo1
miwase4
misrse4
11
misrmo4
miwadm4
miwssd4
misbse4
masrmo1
masrmo2
misbse2
misbse1
miwadm1

Figure 42. Redundancy Analysis for the **foraging mode/body size** approach, using √√-transformed abundance data. Sample points (■) are labelled with station numbers (see Table 1), biological variables (●) with lowercase alphanumeric codes (see Figure 2 for explanation of variable codes), and environmental variables (↦) with uppercase labels (abbreviation of variable name). Biological variables situated outside the range of sample points in the ordination are indicated by a small arrow next to the variable code. Scaling factor of environmental biplot scores= 3.74.

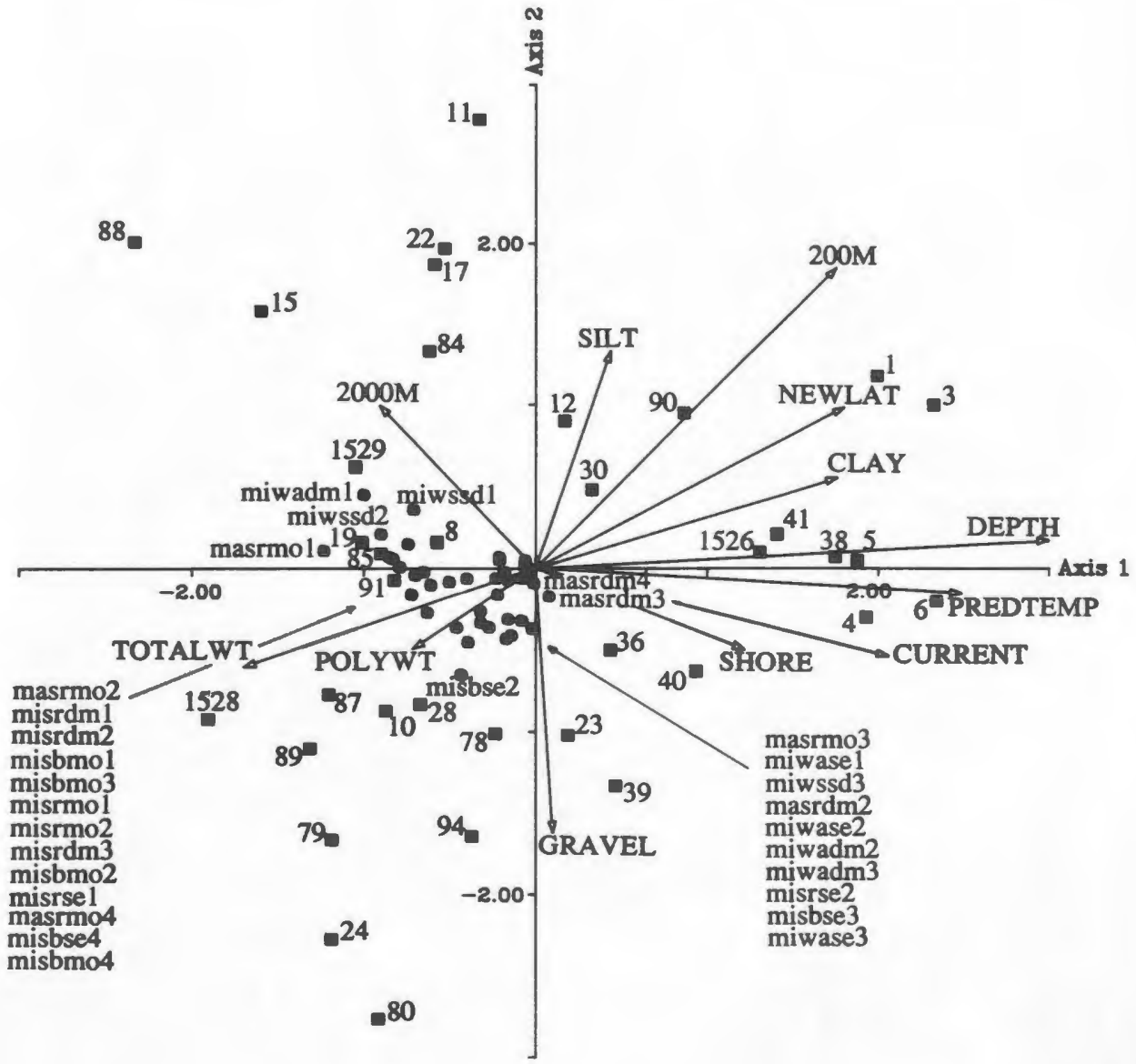

Axis 2
Axis 1
2.00
-2.00
2.00
-2.00
11
88
22
17
15
84
2000M
1529
miwadm1
miwssd1
miwssd2
masrmo1
19
8
85
91
SILT
12
30
200M
90
NEWLAT
1
3
CLAY
41
1526
38
5
DEPTH
masrdm4
masrdm3
6
PREDTEMP
4
36
SHORE
40
CURRENT
TOTALWT
POLYWT
misbse2
masrmo2
misrdm1
misrdm2
misbmo1
misbmo3
misrmo1
misrmo2
misrdm3
misbmo2
misrse1
masrmo4
misbse4
misbmo4
1528
87
28
10
78
89
79
94
24
80
23
39
GRAVEL
masrmo3
miwase1
miwssd3
masrdm2
miwase2
miwadm2
miwadm3
misrse2
misbse3
miwase3

Figure 43. Cumulative proportion of variance explained by the first four axes and by all axes (trace) of Principal Components Analysis and Redundancy Analysis for the **foraging mode/body size** approach, using √√-transformed abundance data.

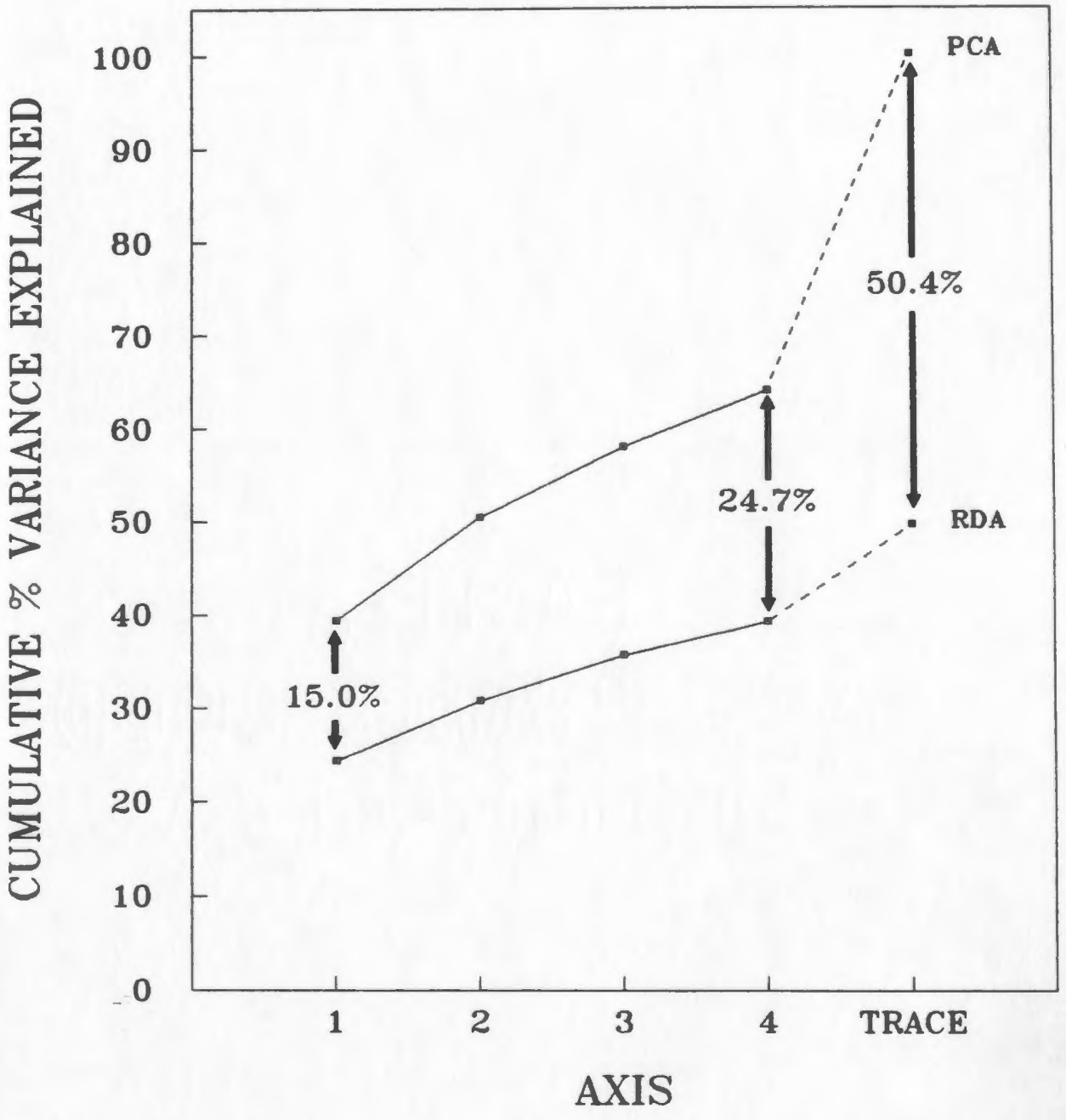

CUMULATIVE % VARIANCE EXPLAINED
100
90
80
70
60
50
40
30
20
10
0
1
2
3
4
TRACE
AXIS
PCA
RDA
50.4%
24.7%
15.0%

Figure 44. Multidimensional scaling ordination of samples based on the **foraging mode/body size** approach, using arcsin$\sqrt{}$-transformed percentage data (stress value for two dimensions: 0.25). UPGMA groupings are represented by the envelopes around the samples. Data points are labelled with the station number as listed in Table 1.

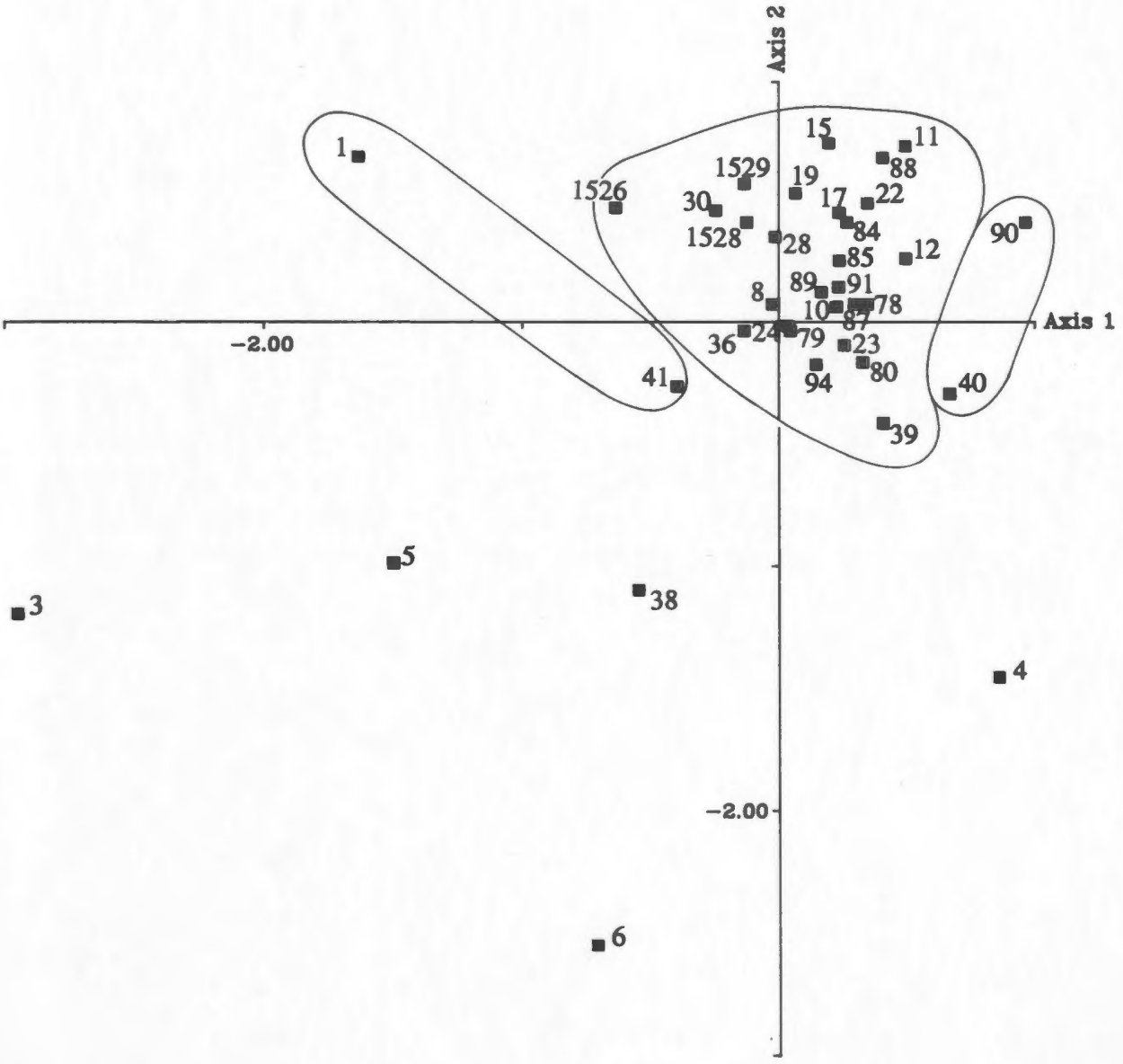

Axis 2
Axis 1
-2.00
-2.00
1
15
11
1529
88
19
1526
30
17
22
84
1528
28
90
85
12
89
91
8
10
78
87
36
24
79
23
41
94
80
40
39
5
3
38
4
6

Figure 45. Principal Components Analysis for the **foraging mode/body size** approach, using $\log_e$-transformed percentage data. Sample points (■) are labelled with station numbers (see Table 1) and biological variables (●) with lowercase alphanumeric codes. See Figure 2 for explanation of variable codes. Variables situated outside the range of sample points in the ordination are indicated by a small arrow next to the variable code.

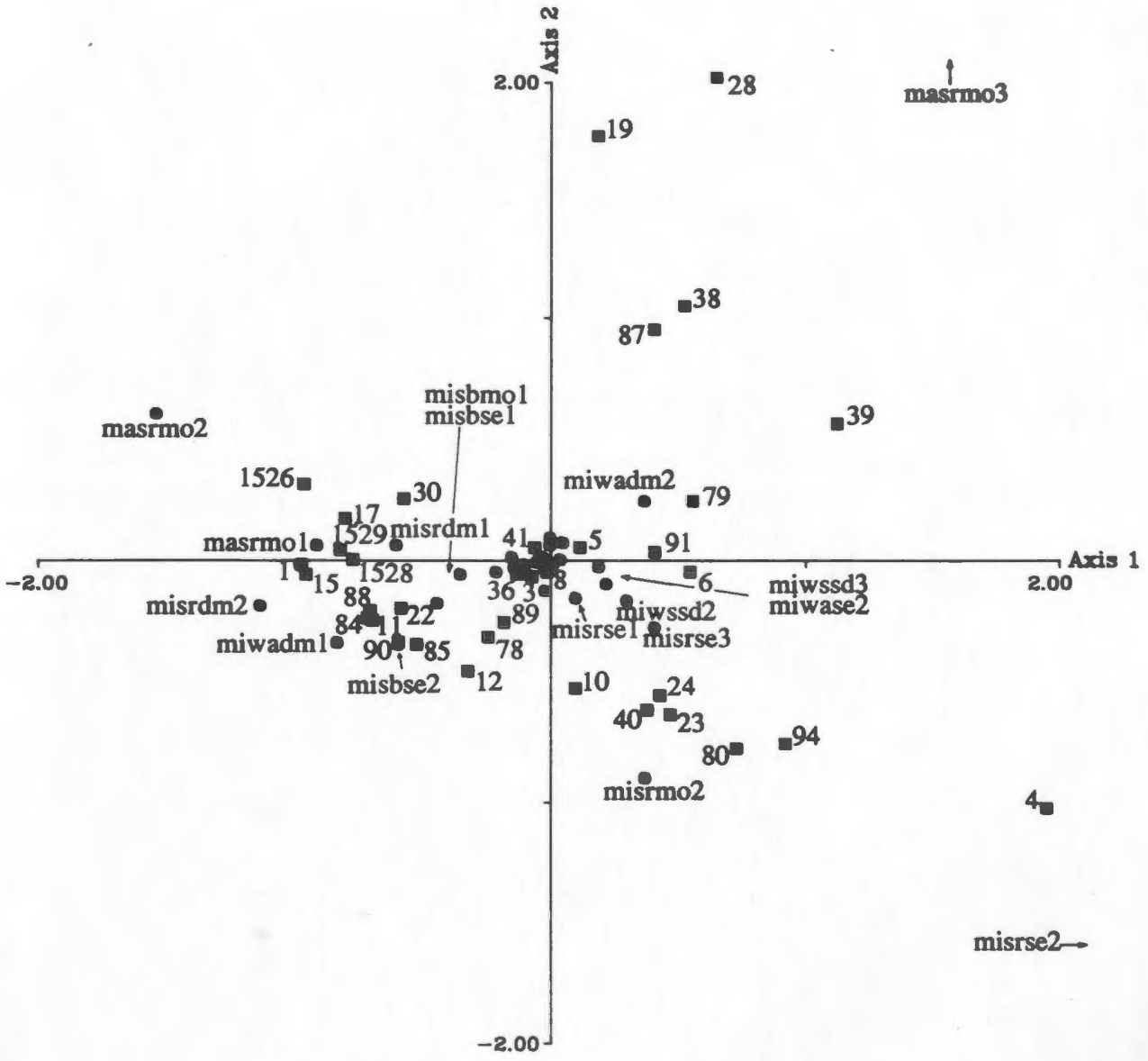

Axis 2
2.00
-2.00
Axis 1
-2.00
2.00
28
masrmo3
19
38
87
misbmo1
misbse1
masrmo2
39
1526
30
miwadm2
79
17
masrmo1
1529
misrdm1
41
5
91
1
15
1528
36
3
8
6
miwssd3
miwase2
misrdm2
88
84
1
22
89
miwssd2
misrse1
misrse3
miwadm1
90
85
78
misbse2
12
10
24
40
23
94
80
misrmo2
4
misrse2

Figure 46. Redundancy Analysis for the **foraging mode/body size** approach, using $\log_e$-transformed percentage data. Sample points (■) are labelled with station numbers (see Table 1), biological variables (●) with lowercase alphanumeric codes (see Figure 2 for explanation of variable codes), and environmental variables (↦) with uppercase labels (abbreviation of variable name). Biological variables situated outside the range of sample points in the ordination are indicated by a small arrow next to the variable code. Scaling factor of environmental biplot scores= 4.38.

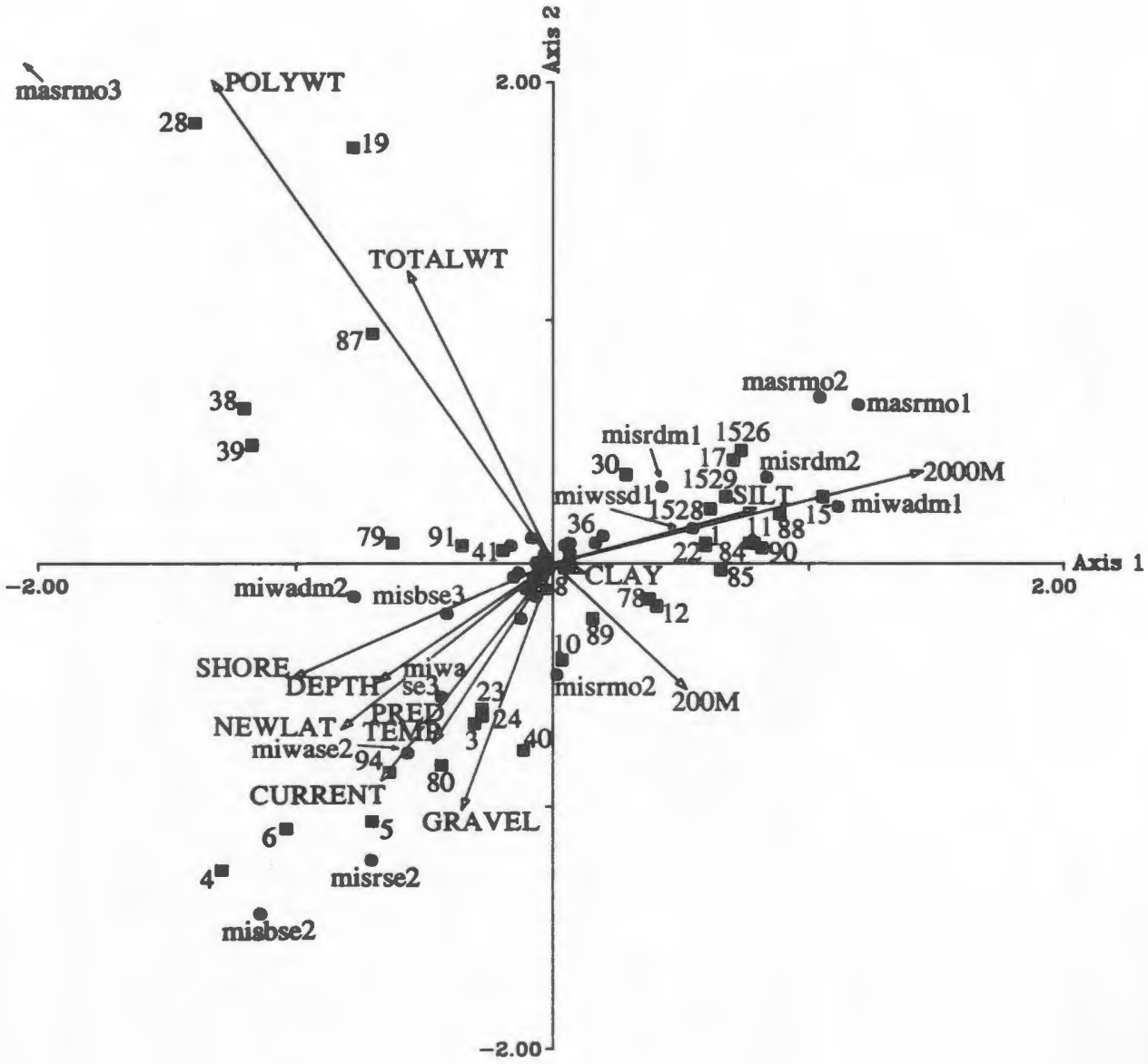

Axis 2
2.00
-2.00
Axis 1
-2.00
2.00
masrmo3
POLYWT
28
19
TOTALWT
87
38
39
masrmo2
masrmo1
misrdm1
1526
17
misrdm2
30
1529
2000M
miwssd1
SILT
1528
15
miwadm1
36
11
88
79
91
41
22
84
90
CLAY
85
miwadm2
misbse3
78
12
89
10
SHORE
DEPTH
miwa
se3
misrmo2
200M
23
PRED
NEWLAT
TEMP
24
3
40
miwase2
94
80
CURRENT
GRAVEL
6
5
4
misrse2
misbse2

Figure 47. Cumulative proportion of variance explained by the first four axes and by all axes (trace) of Principal Components Analysis and Redundancy Analysis for the **foraging mode/body size** approach, using $\log_e$-transformed percentage data.

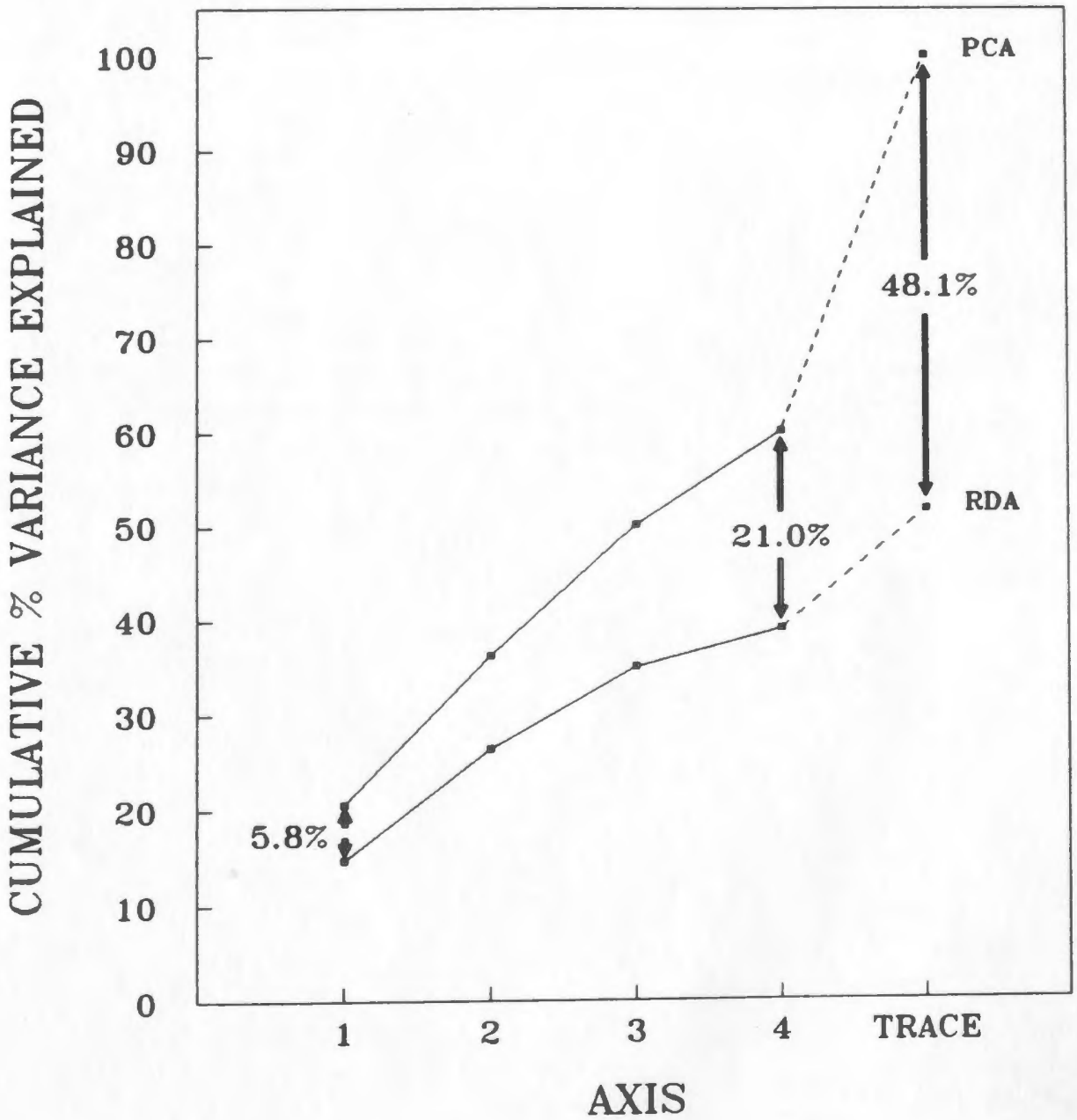

CUMULATIVE % VARIANCE EXPLAINED
100
90
80
70
60
50
40
30
20
10
0
1
2
3
4
TRACE
AXIS
PCA
RDA
48.1%
21.0%
5.8%

Figure 48. Multidimensional scaling ordination of samples based on the **taxonomic** approach, using √√-transformed abundance data (stress value for two dimensions: 0.28). UPGMA groupings are represented by the envelopes around the samples. Data points are labelled with the station number as listed in Table 1.

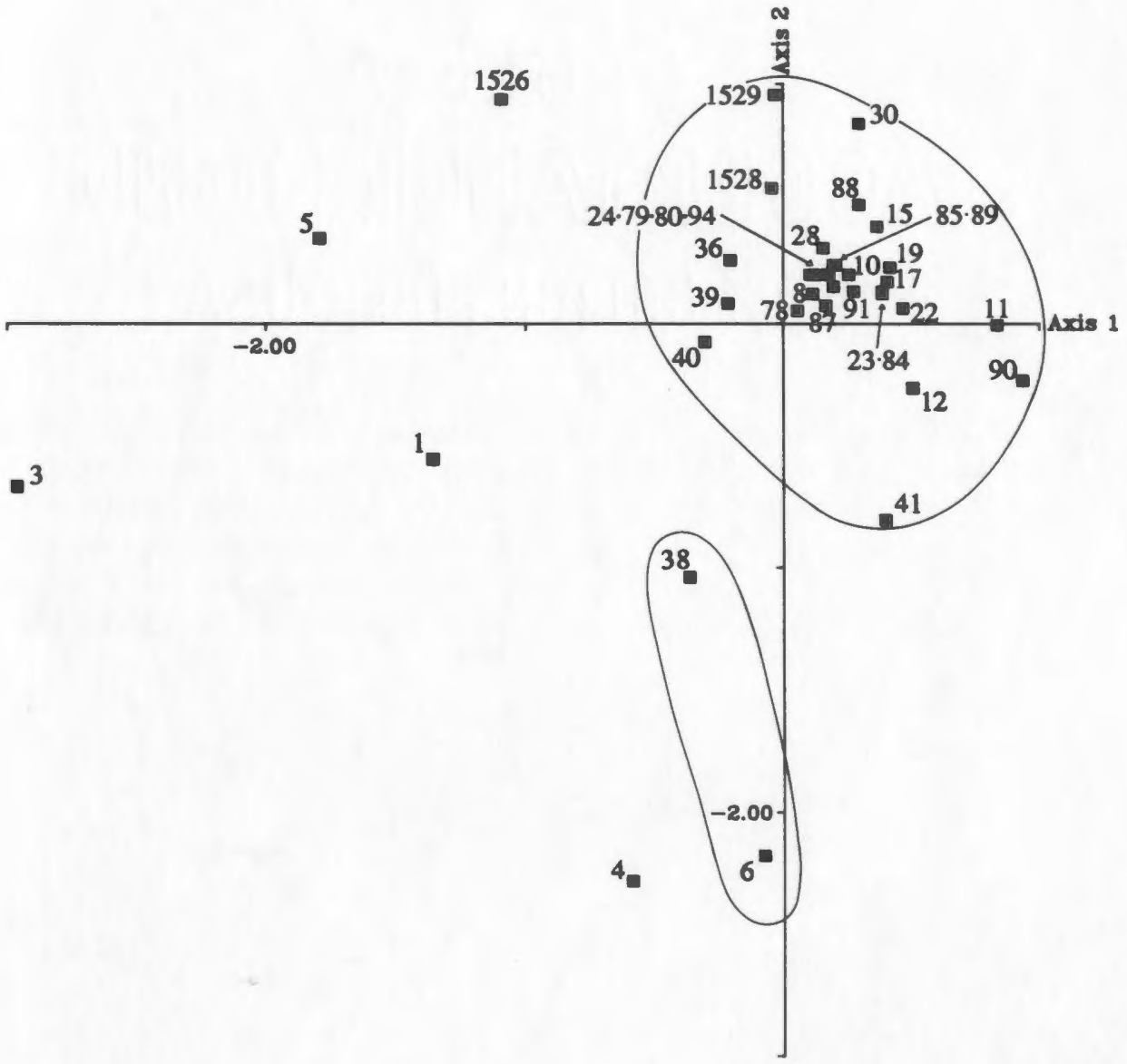

Axis 2
Axis 1
1526
1529
30
1528
88
15
85·89
24·79·80·94
28
36
19
10
17
39
8
78
91
87
22
11
5
−2.00
40
23·84
90
12
1
3
41
38
−2.00
4
6

Figure 49. Principal Components Analysis for the **taxonomic** approach, using √√-transformed abundance data. Sample points (■) are labelled with station numbers (see Table 1) and biological variables (●) with lowercase alphanumeric codes. See Figure 2 for explanation of variable codes. Variables situated outside the range of sample points in the ordination are indicated by a small arrow next to the variable code.

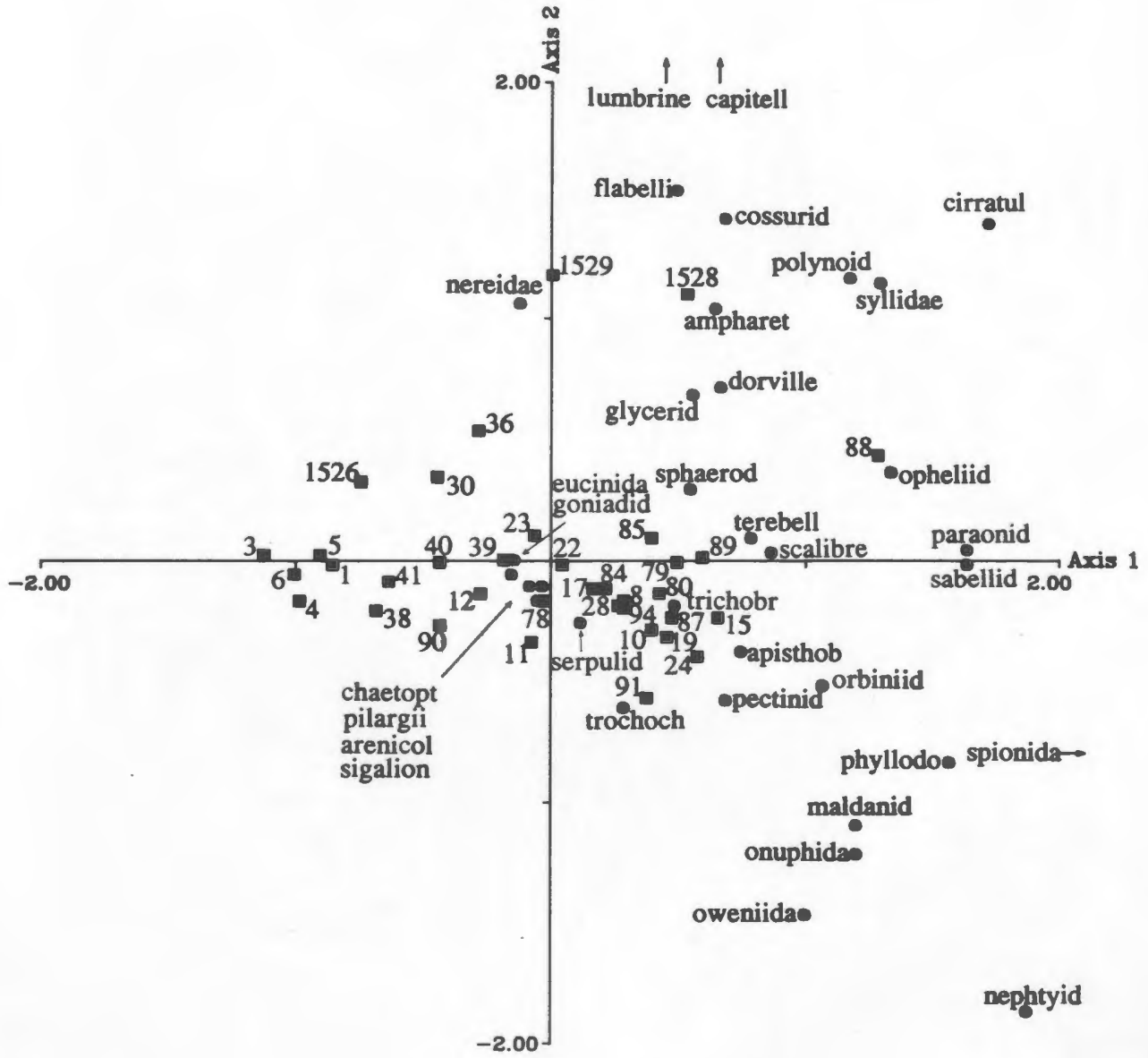

Axis 2
2.00
lumbrine
capitell
flabelli
cossurid
cirratul
1529
nereidae
1528
polynoid
syllidae
ampharet
dorville
glycerid
36
88
opheliid
1526
30
eucinida
sphaerod
goniadid
23
85
terebell
paraonid
3
5
40
39
22
89
scalibre
Axis 1
-2.00
6
1
41
84
79
80
sabellid
2.00
4
12
17
28
8
trichobr
38
78
94
87
15
90
11
10
19
serpulid
24
apisthob
91
orbiniid
chaetopt
pilargii
arenicol
sigalion
pectinid
trochoch
phyllodo
spionida
maldanid
onuphida
oweniida
nephtyid
-2.00

Figure 50. Redundancy Analysis for the **taxonomic** approach, using √√-transformed abundance data. Sample points (■) are labelled with station numbers (see Table 1), biological variables (●) with lowercase alphanumeric codes (see Figure 2 for explanation of variable codes), and environmental variables (↦) with uppercase labels (abbreviation of variable name). Biological variables situated outside the range of sample points in the ordination are indicated by a small arrow next to the variable code. Scaling factor of environmental biplot scores= 2.45.

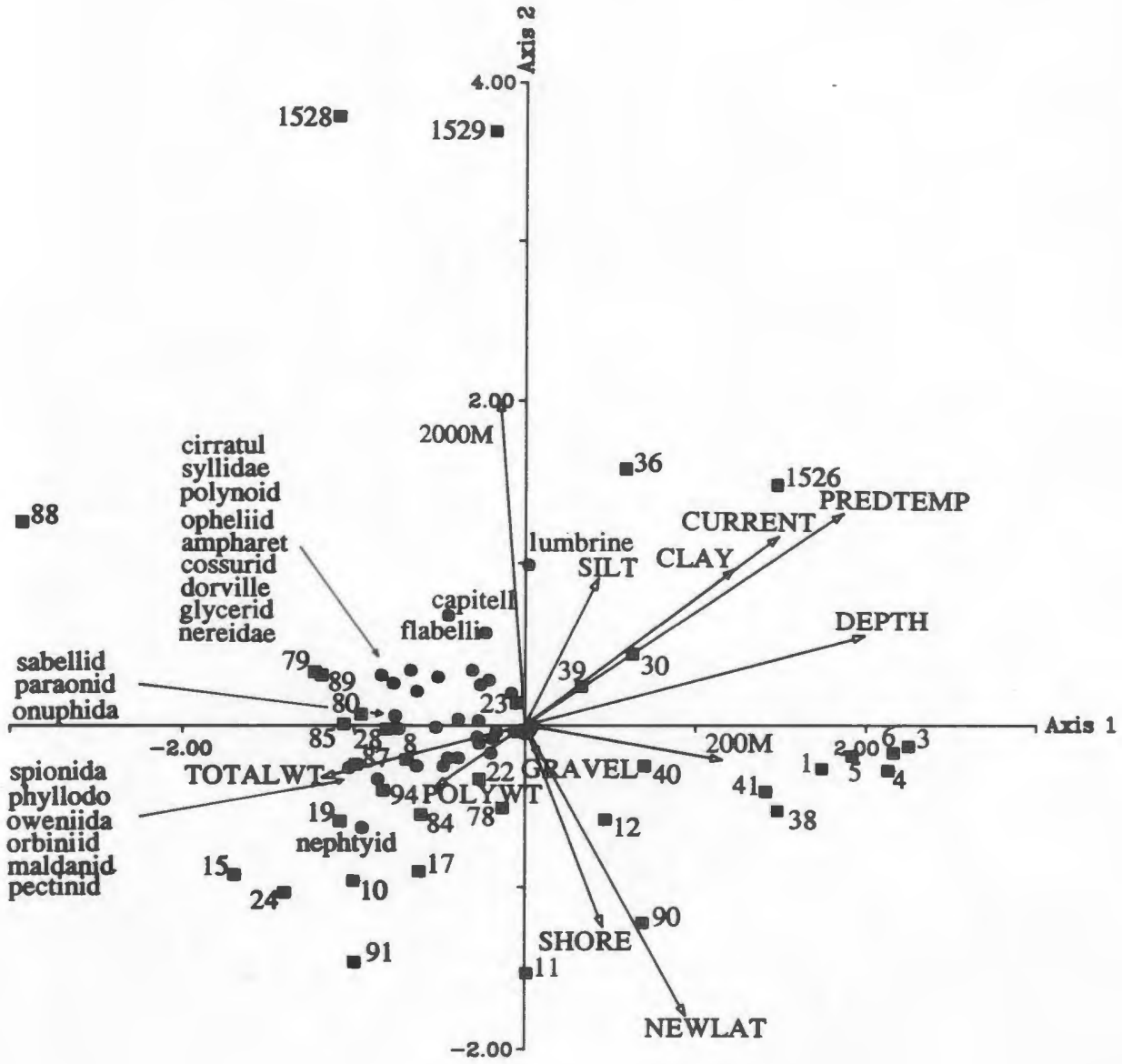

Axis 2
4.00
2.00
-2.00
Axis 1
-2.00
2.00
200M
2000M
1528
1529
36
1526
PREDTEMP
CURRENT
CLAY
SILT
lumbrine
DEPTH
88
cirratul
syllidae
polynoid
opheliid
ampharet
cossurid
dorville
glycerid
nereidae
capitell
flabelli
sabellid
paraonid
onuphida
spionida
phyllodo
oweniida
orbiniid
maldanid
pectinid
TOTALWT
GRAVEL
POLYWT
nephtyid
SHORE
NEWLAT
79
89
80
85
28
87
8
23
39
30
22
94
84
78
19
17
10
24
15
91
11
90
12
40
41
38
1
5
4
6
3

Figure 51. Cumulative proportion of variance explained by the first four axes and by all axes (trace) of Principal Components Analysis and Redundancy Analysis for the **taxonomic** approach, using √√-transformed abundance data.

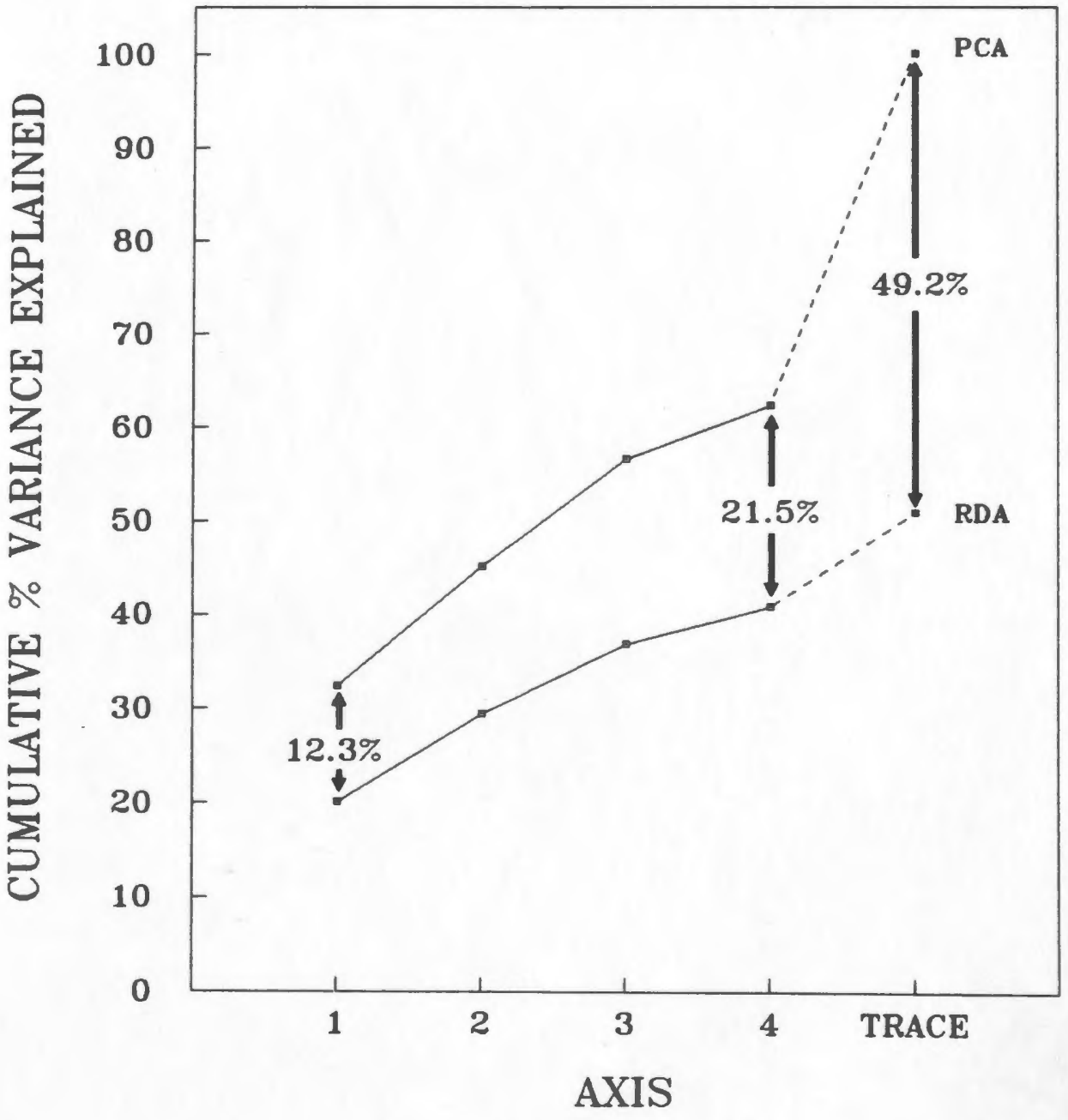

CUMULATIVE % VARIANCE EXPLAINED
100
90
80
70
60
50
40
30
20
10
0
1
2
3
4
TRACE
AXIS
PCA
RDA
49.2%
21.5%
12.3%

Figure 52. Multidimensional scaling ordination of samples based on the **taxonomic** approach, using arcsin$\sqrt{}$-transformed percentage data (stress value for two dimensions: 0.35). UPGMA groupings are represented by the envelopes around the samples. Data points are labelled with the station number as listed in Table 1.

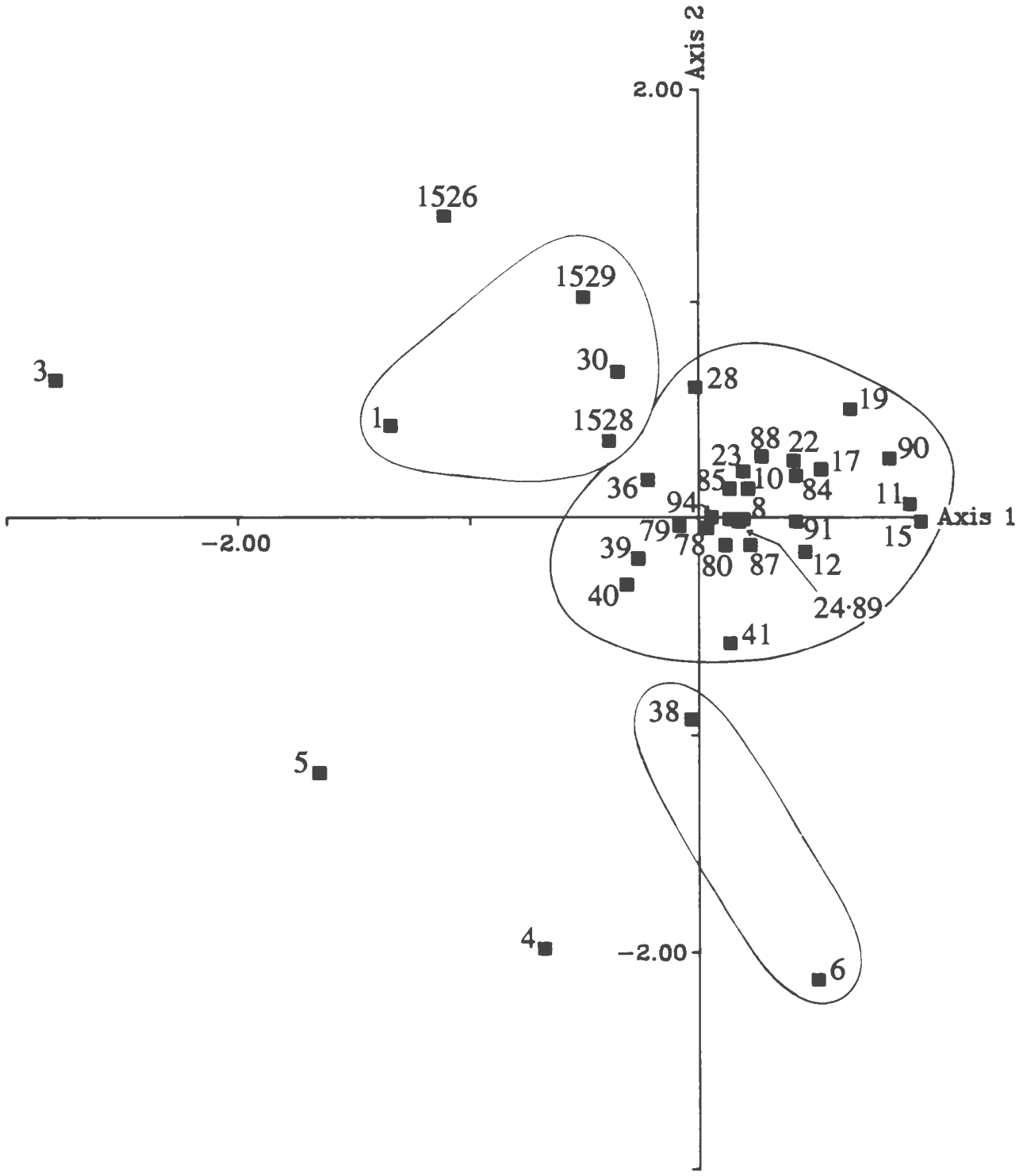

Axis 2
2.00
-2.00
Axis 1
-2.00
1526
1529
30
3
28
19
1
1528
88
22
23
17
90
36
85
10
84
11
94
8
79
78
91
15
39
80
87
12
40
24·89
41
38
5
4
6

Figure 53. Principal Components Analysis for the **taxonomic** approach, using $\log_e$-transformed percentage data. Sample points (■) are labelled with station numbers (see Table 1) and biological variables (●) with lowercase alphanumeric codes. See Figure 2 for explanation of variable codes. Variables situated outside the range of sample points in the ordination are indicated by a small arrow next to the variable code.

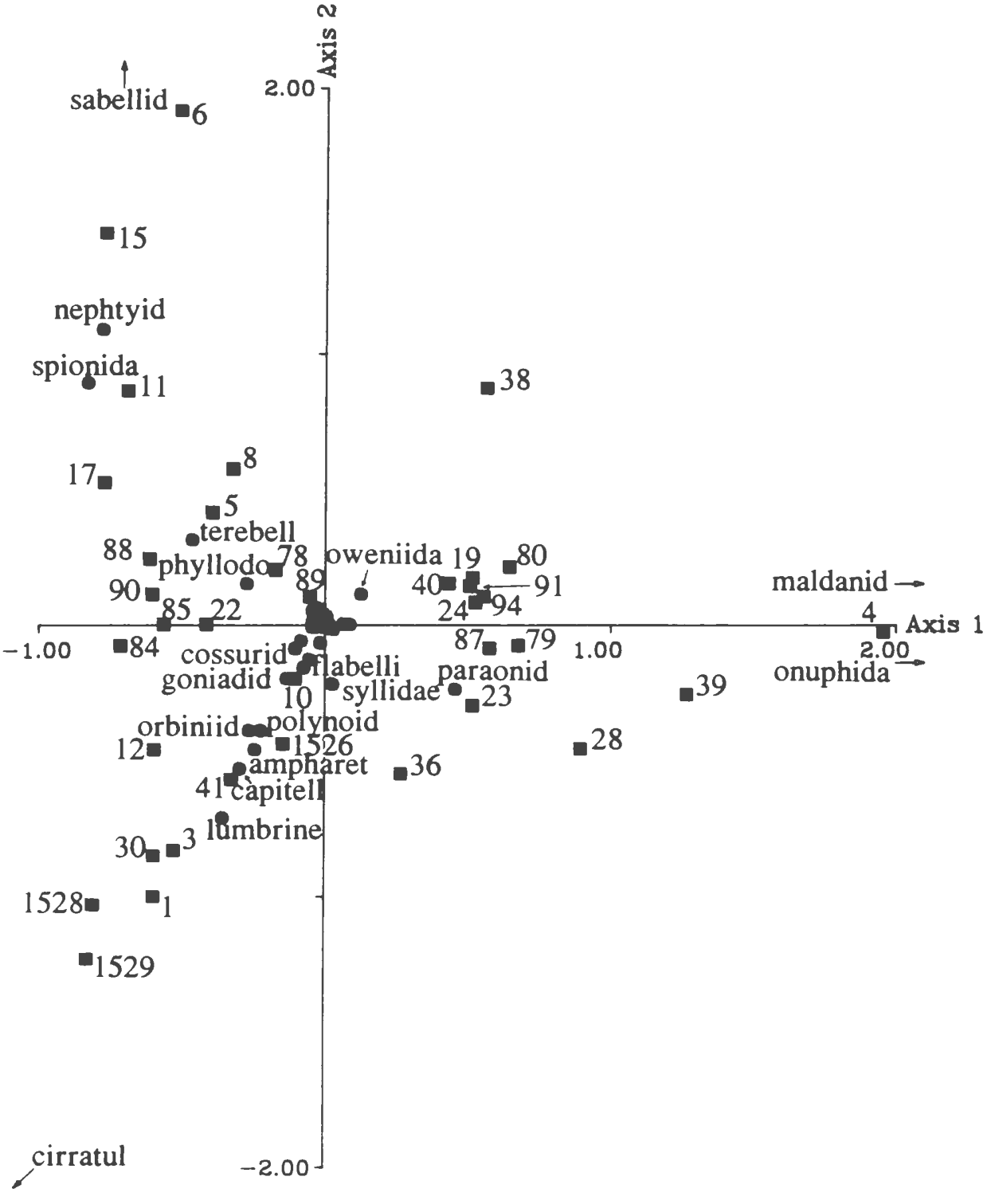

Axis 2
2.00
−2.00
−1.00
1.00
2.00
Axis 1
sabellid
6
15
nephtyid
spionida
11
38
17
8
5
terebell
88
phyllodo
78
oweniida
19
80
90
89
40
91
maldanid
85
22
24
94
4
84
87
79
cossurid
flabelli
goniadid
paraonid
onuphida
10
syllidae
23
39
orbiniid
polynoid
12
1526
28
ampharet
36
41
capitell
lumbrine
30
3
1528
1
1529
cirratul

Figure 54. Redundancy Analysis for the **taxonomic** approach, using $\log_e$-transformed percentage data. Sample points (■) are labelled with station numbers (see Table 1), biological variables (●) with lowercase alphanumeric codes (see Figure 2 for explanation of variable codes), and environmental variables (↦) with uppercase labels (abbreviation of variable name). Biological variables situated outside the range of sample points in the ordination are indicated by a small arrow next to the variable code. Scaling factor of environmental biplot scores= 3.85.

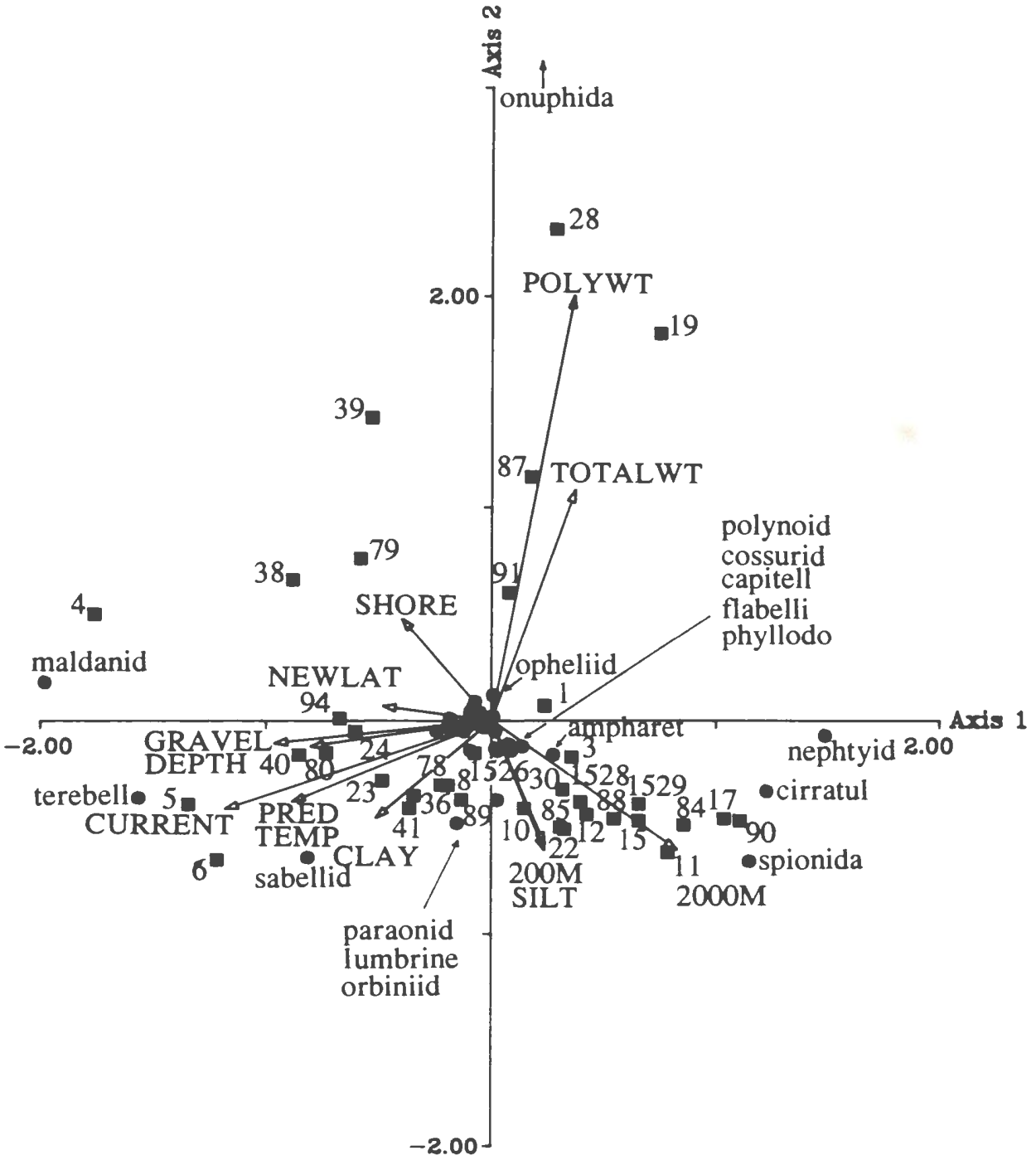
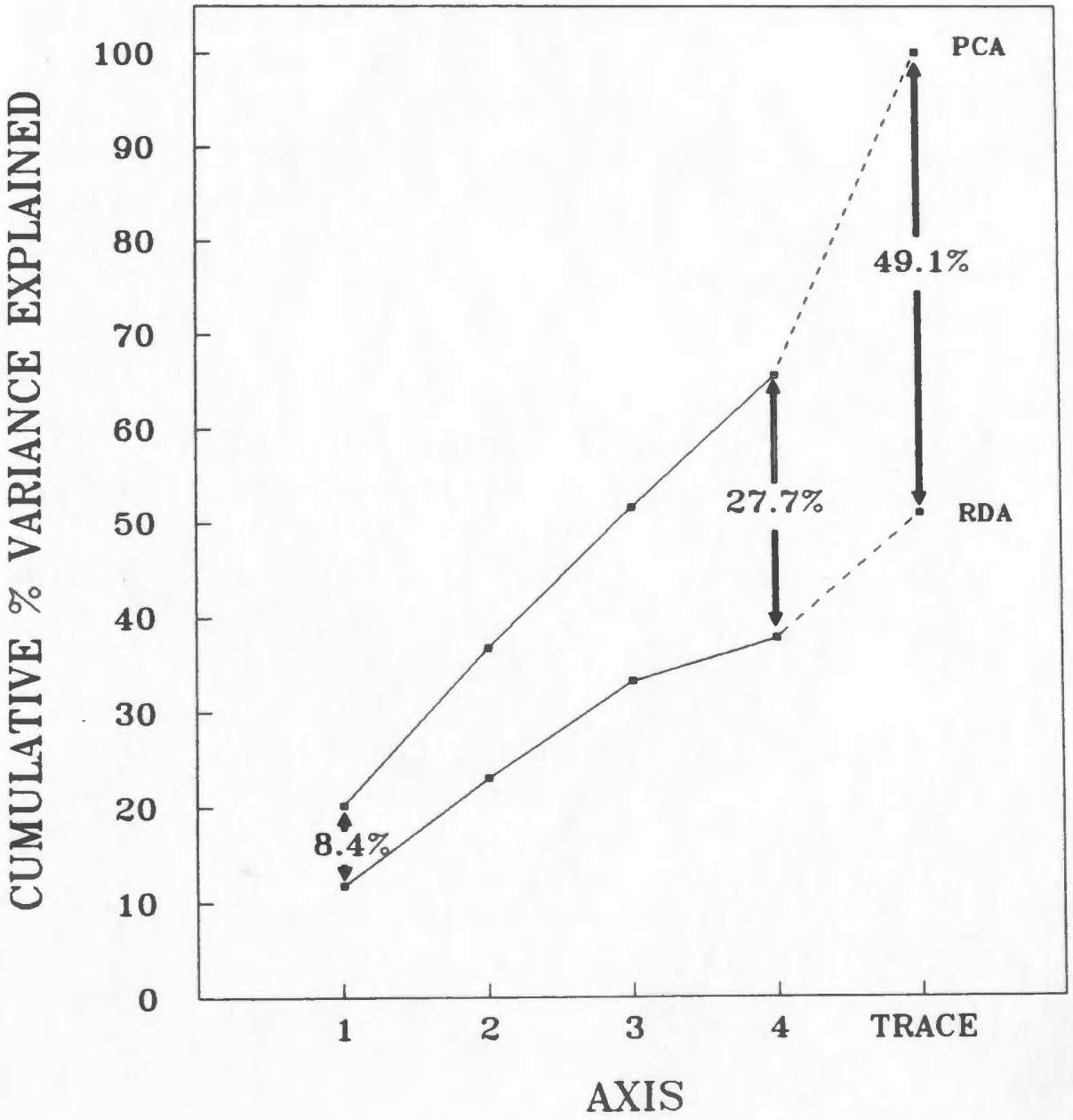

Axis 2
onuphida
28
POLYWT
2.00
19
39
87
TOTALWT
polynoid
cossurid
capitell
flabelli
phyllodo
79
38
91
SHORE
4
maldanid
opheliid
NEWLAT
94
1
Axis 1
ampharet
−2.00
GRAVEL
DEPTH
40
80
24
78
8
152
6
30
3
1528
1529
nephtyid
2.00
terebell
5
23
36
89
85
88
84
17
cirratul
CURRENT
PRED
TEMP
41
10
12
15
90
6
sabellid
CLAY
22
11
spionida
200M
SILT
2000M
paraonid
lumbrine
orbiniid
−2.00

Figure 55. Cumulative proportion of variance explained by the first four axes and by all axes (trace) of Principal Components Analysis and Redundancy Analysis for the **taxonomic** approach, using $\log_e$-transformed percentage data.


CUMULATIVE % VARIANCE EXPLAINED
100
90
80
70
60
50
40
30
20
10
0
1
2
3
4
TRACE
AXIS
PCA
RDA
49.1%
27.7%
8.4%

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APPENDICES

Appendix A

Measuring system: hardware, software, and operation

Digitizing system VERSAPAD, version BENTHOPAD

The VERSAPAD digitizing system (hardware setup and software) was designed to accelerate ecological measurements, which are often numerous and repetitive. We have attempted to reduce the number of interactions with the keyboard to a minimum while using the maximum graphic capability of an Apple II+.

Hardware

- Apple II+ 64K RAM microcomputer and b/w monitor
- Floppy disk drive I
- Super Serial Port card
- Memory expansion card (Language card; optional)
- Accelerator card (e.g. TRANSWARP; optional) and micro-fan
- HIPAD digitizing tablet (Houston Instruments), with 4-button cursor (any other tablet or cursor can be used with minimal change to program).

Software and operation

Program VERSAPAD, version BENTHOPAD, on DIVERSI-DOS

Unlike many digitizing sotfware that have a series of screen menus to call the different routines of the program, we have used a small portion of the digitizing space on the tablet for a menu (similar to the Zeiss approach). The tablet HIPAD uses a 4-button cross-hair cursor. The program, however, can be adapted for a 2-button cursor or a stylus.

The tablet menu consists of 7 distinct areas: 6 functions (color coded) and a coding series (codes 1 to 20). Each function can be called for by pressing a given key on the cursor when the latter is situated on the desired area on the menu.

- ENTER DATA - informs the program that the next entry(ies) will be a measurement.
- SPECIES - allows rapid change of species code by calling the corresponding routine. Species codes can be entered through the keyboard, the cursor or automatically (from 1 up).
- PICTURE - calls the scaling routine to enter scales manually or automatically.
- STATION - allows change of station (or sample) number and other related information (e.g. depth, date).
- VISUALIZE - displays the current data or data previously stored in memory.
- OUTPUT - sends the current data to memory storage or saves the data from memory onto diskette.
- Coding series - a series of 20 numbered cells allows rapid entry of species code and scaling code. Using a neat trick, the number of

codes that can be obtained from the limited number of cells becomes virtually infinite.

When the program starts, a few general questions are asked:

1. Do you want to adjust the video proportions ? This allows proportional video (screen) image to the space used on the tablet.
2. Do you want to enter species code with cursor, keyboard or automatically (from 1 up) ?
3. Do you want to enter scaling factor manually (i.e. each time you need to change) or automatically (i.e. entered only once here and later referred to by a code on the tablet menu) ?
4. Which unit of measurement (from micrometres to kilometres) will you use ?

Then, the program will prompt the user to give station (or sample) number, station depth, species code, scaling factor (as a code or in full) and any other questions introduced in the program. VERSAPAD is an open program. Its simple BASIC format allows rapid modification and expansion if necessary. However, most problems in ecology can be addressed without modification to the original design.

Once the detailled information on each station/sample (or picture) has been entered, it is time to ENTER DATA, or start measuring. By pressing any cursor key when the cursor (cross-hair) is situated on ENTER DATA, the program awaits for values (points) coming from the tablet. These points are then interpreted for straight length, curved length, diameter, surface-area or coordinates, depending on the key pressed on the cursor and on the switch setup on the tablet (i.e. point mode or switch stream mode). In a few seconds, one can measure the length, diameter and surface-area of an object and send it to

memory by pressing the white key with the cursor on OUTPUT. It is possible to view the set of measurements for the last entry, before sending it to memory, by pressing the white key with cursor on VISUALIZE. If the user is satisfied, the data can then be sent to memory. By pressing the red key with cursor on VISUALIZE, the user can also access a screen menu to view, modify or eliminate any of the previous entries before they are saved on the diskette.

A typical sequence of measurements would then be:

1. white cursor-key on ENTER DATA
2. 2 points (point mode) for diameter with green cursor-key
3. white cursor-key on ENTER DATA
4. series of points (switch stream mode) for curved length with red cursor-key
5. white cursor-key on ENTER DATA
6. series of points (switch stream mode) for surface-area with green cursor-key
7. white cursor-key on OUTPUT
8. go to step 1 for next case.

After each measurement, the result is displayed under the graphic representation of the measurement. Here, the key factor in time saving is the fact that all measurements are obtained without any interaction with the keyboard, unless you need to change the station number and other related values. Routines to change the species code, the scaling factor or the station number are accessed by pressing a cursor-key on the specific item of the tablet menu.

At the end of a session, or when the memory is full, the data are saved onto a floppy disk. By pressing the red cursor-key on OUTPUT, the output routine

will ask the user 'Do you want to see the CATALOG?' [of files on the diskette] and 'Do you want to create a new data file?' [or append data to an old file]. Data files on the diskette can then be transferred through a Modem to a mainframe computing system for processing and analysis. KERMIT is a standard program to transfer files from micros to mainframes. We have preferred not to analyse the data on the Apple II+ because of obvious limitations (i.e. memory and speed).

Accuracy and precision of measurements

Roff and Hopcroft (*Can. J. Fish. Aquat. Sci.* **43**[1986]:2044-2048) described a measuring system which uses the same HIPAD digitizing tablet, a microscope fitted with a drawing tube and an IBM personal computer instead of an Apple II+. The HIPAD tablet has working dimensions of 25 X 25 cm, of which 25 X 5 cm are used for the tablet menu in the case of VERSAPAD. With a resolution of 0.1 mm for the tablet, Roff and Hopcroft obtained precision values of $\pm 0.25\%$ and $\pm 0.1\%$ for objects that occupy 25% and 4% of the field of view, respectively. They also reported an accuracy of $< \pm 0.25\%$ on repeated measurements for objects occupying 10% of the field of view. Using the conventional method with a microscope eyepiece micrometer, the maximum precision achieved is usually $\pm 3\%$ for an object occupying 25% of the field of view. An other disadvantage of the conventional system is the need to manipulate and straighten curved specimens.

In the present study, the field of view approximated or exceeded the active area of the digitizing tablet. Tests of the precision and accuracy of measurements yielded values similar to those reported by Roff and Hopcroft (1986).

System designed by

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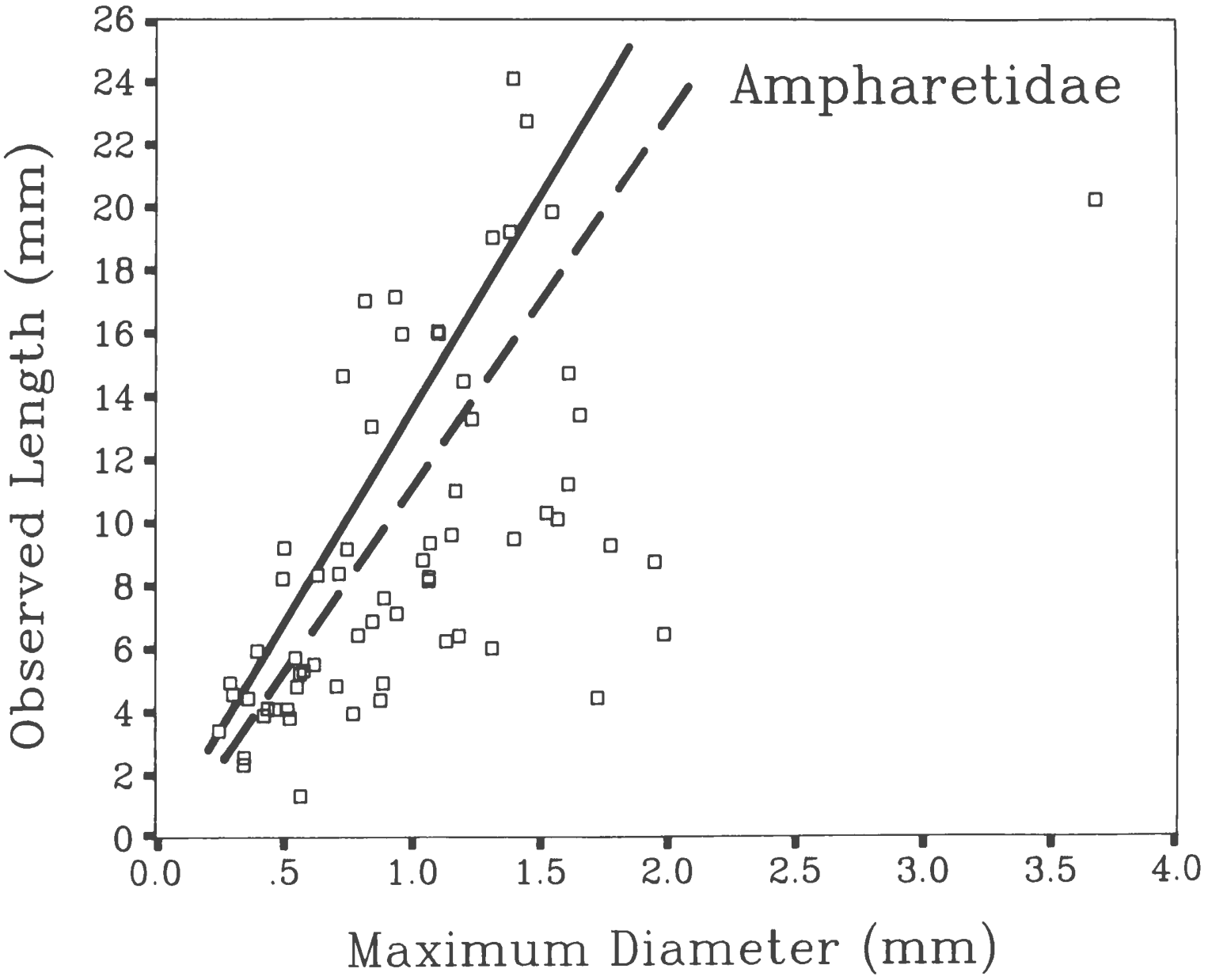
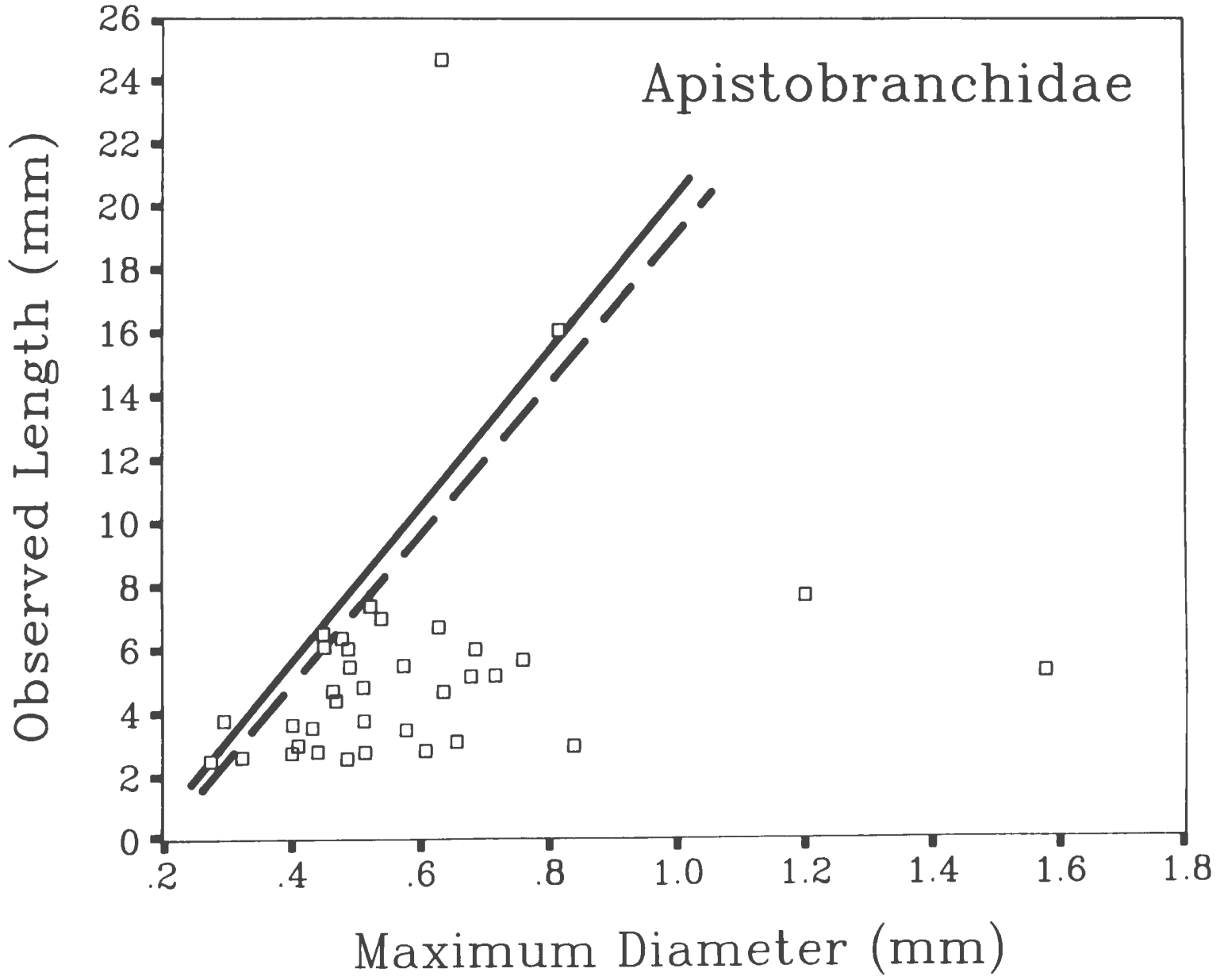
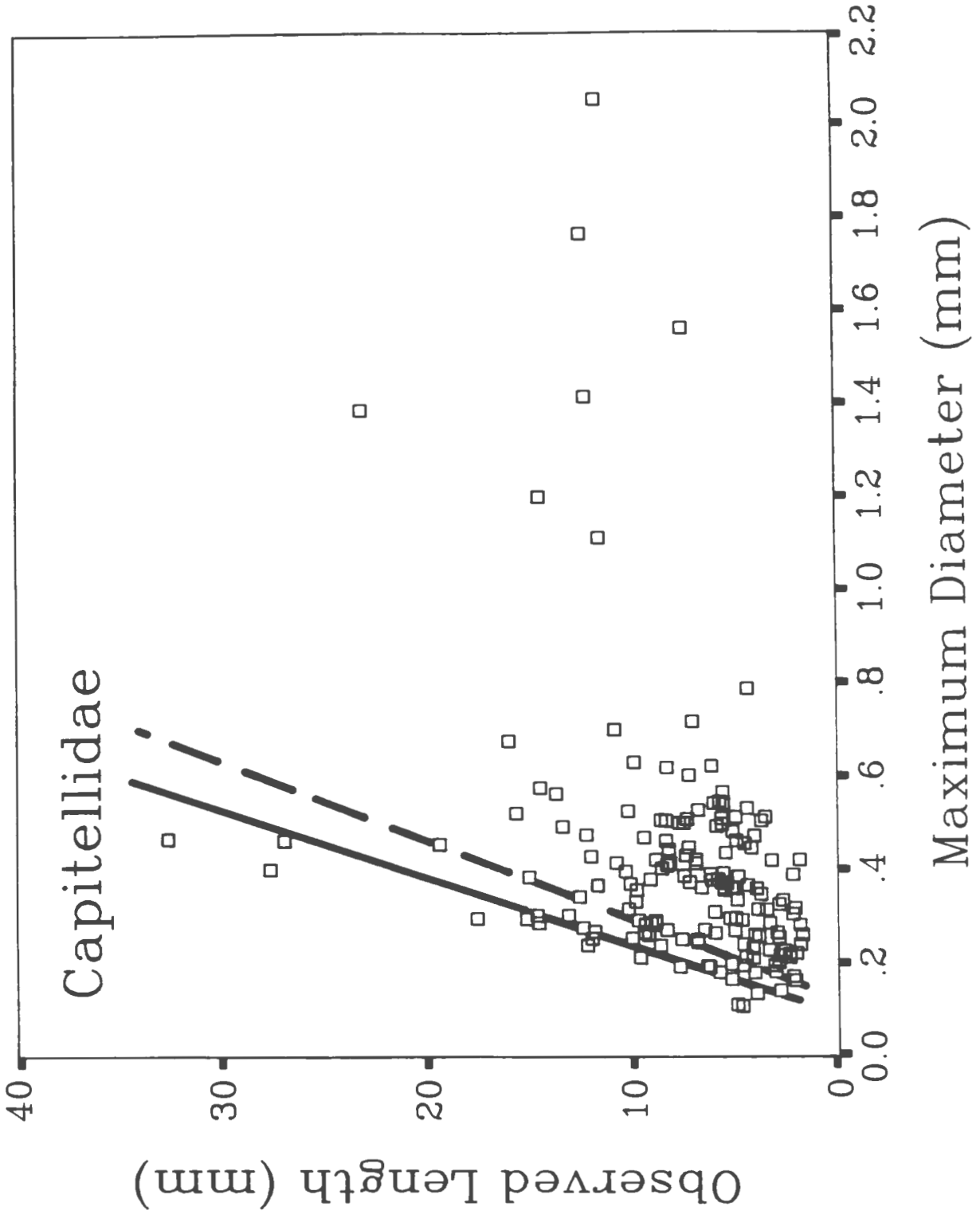
Appendix B

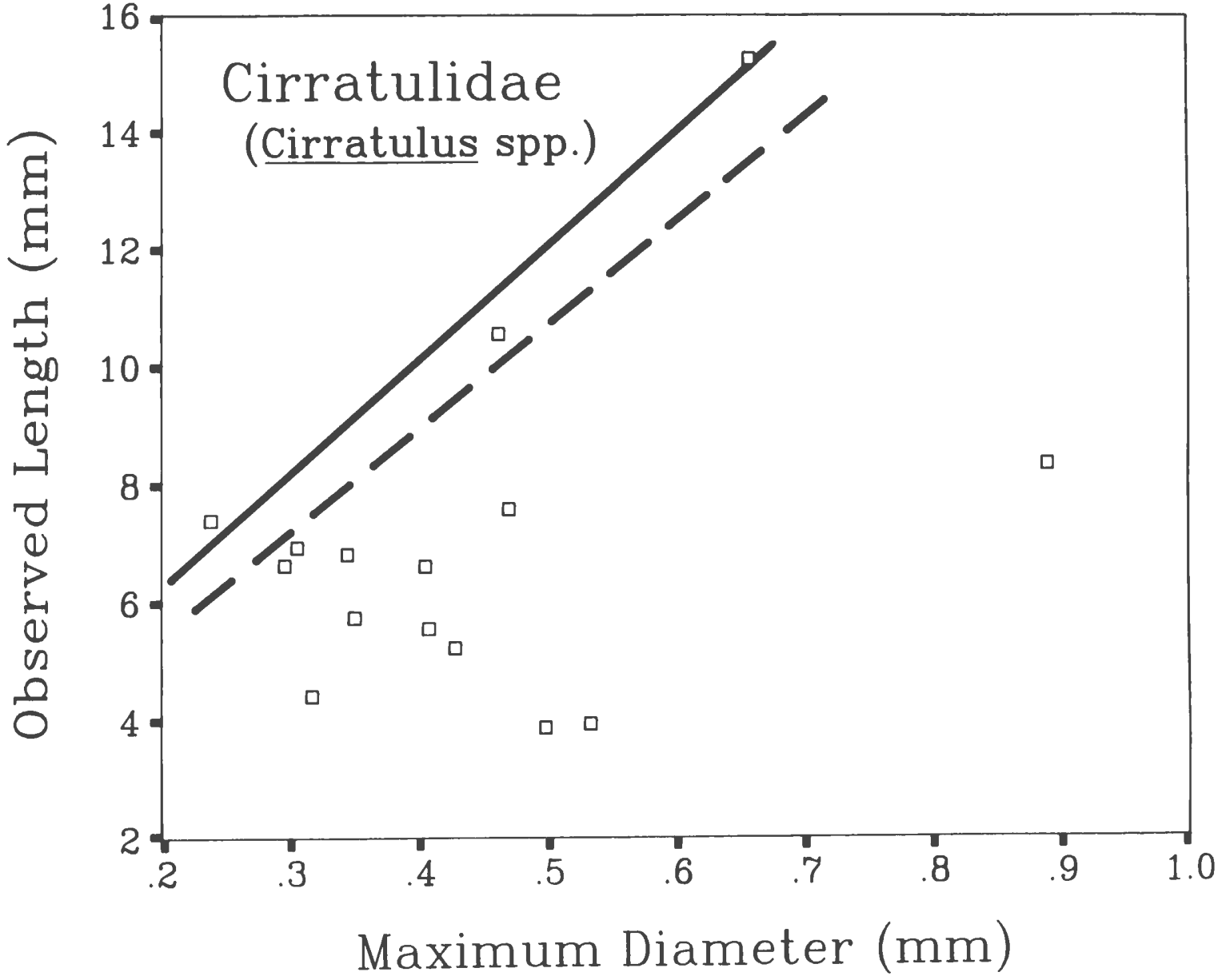
Length / diameter relationship and correction of total body length for truncation

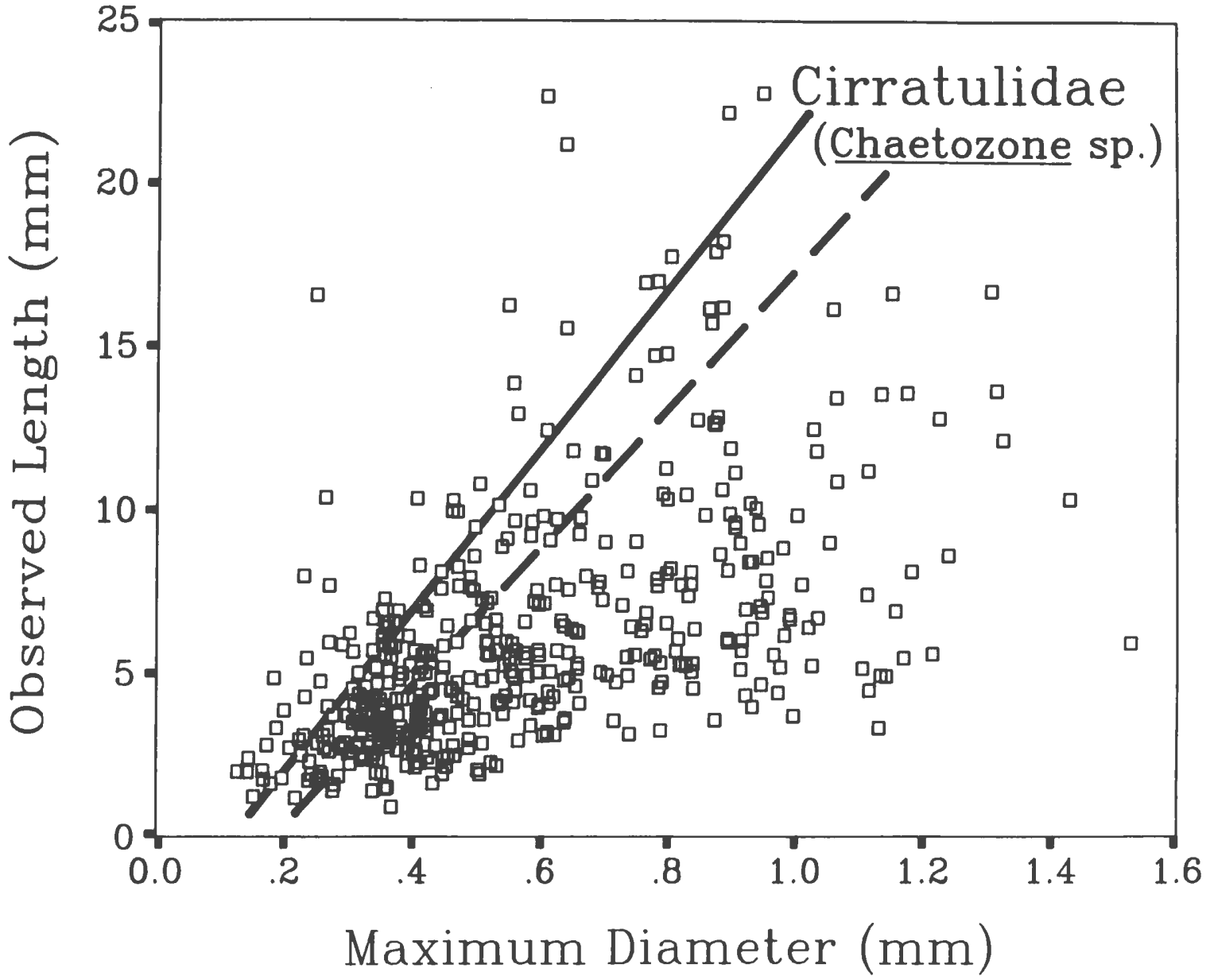
Figures B-1 to B-48. Diagrams of the observed length versus maximum diameter of individual macrobenthic polychaetes for each family from the Labrador shelf and slope and Hermitage Channel. Full line represents estimated length/diameter relationship of non-truncated specimens and dashed line represents cutoff point below which the specimen length is corrected to fit the estimated (non-truncated) length for a given diameter. No correction applied when lines are absent.

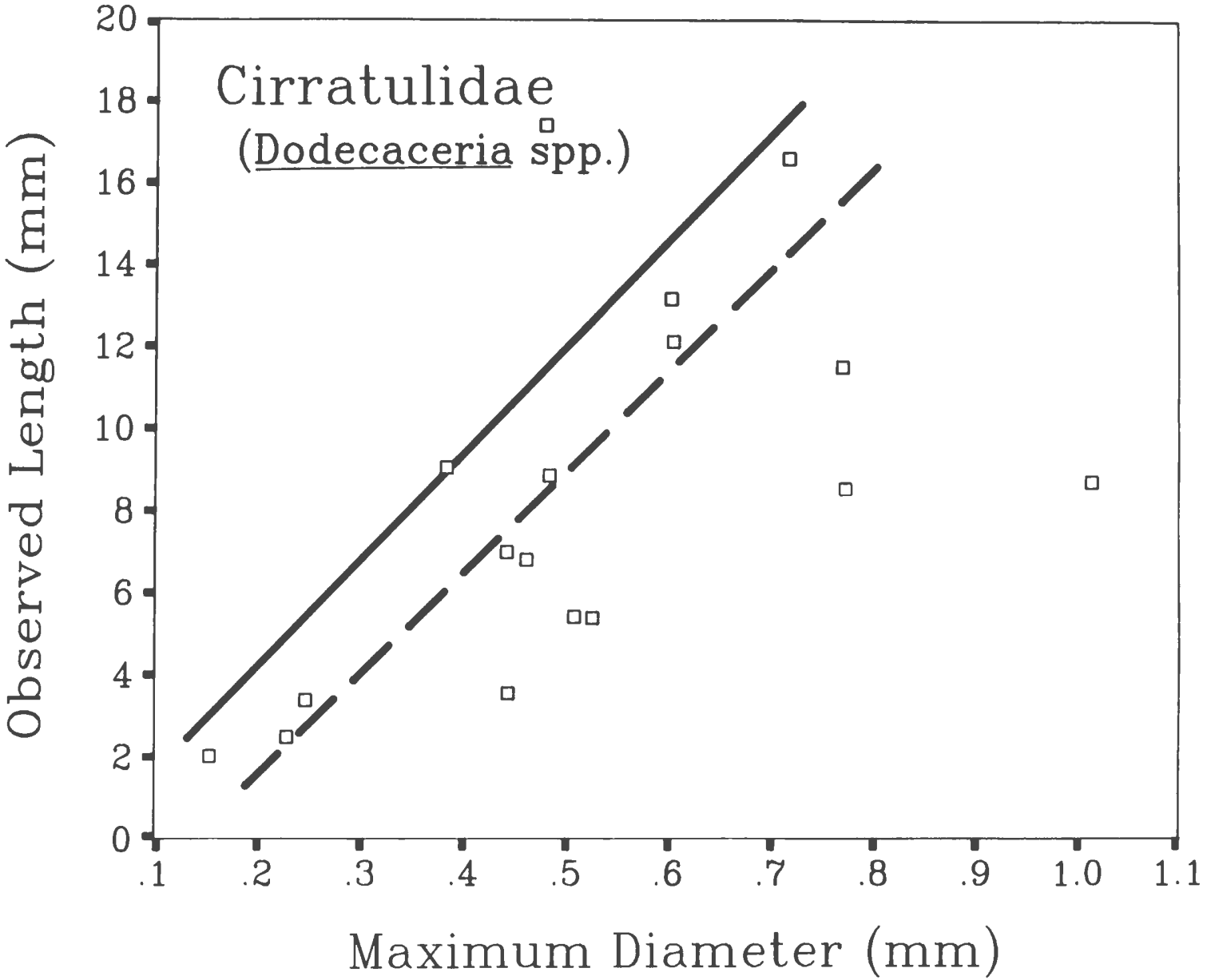

Ampharetidae
Observed Length (mm)
Maximum Diameter (mm)
0
2
4
6
8
10
12
14
16
18
20
22
24
26
0.0
.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0

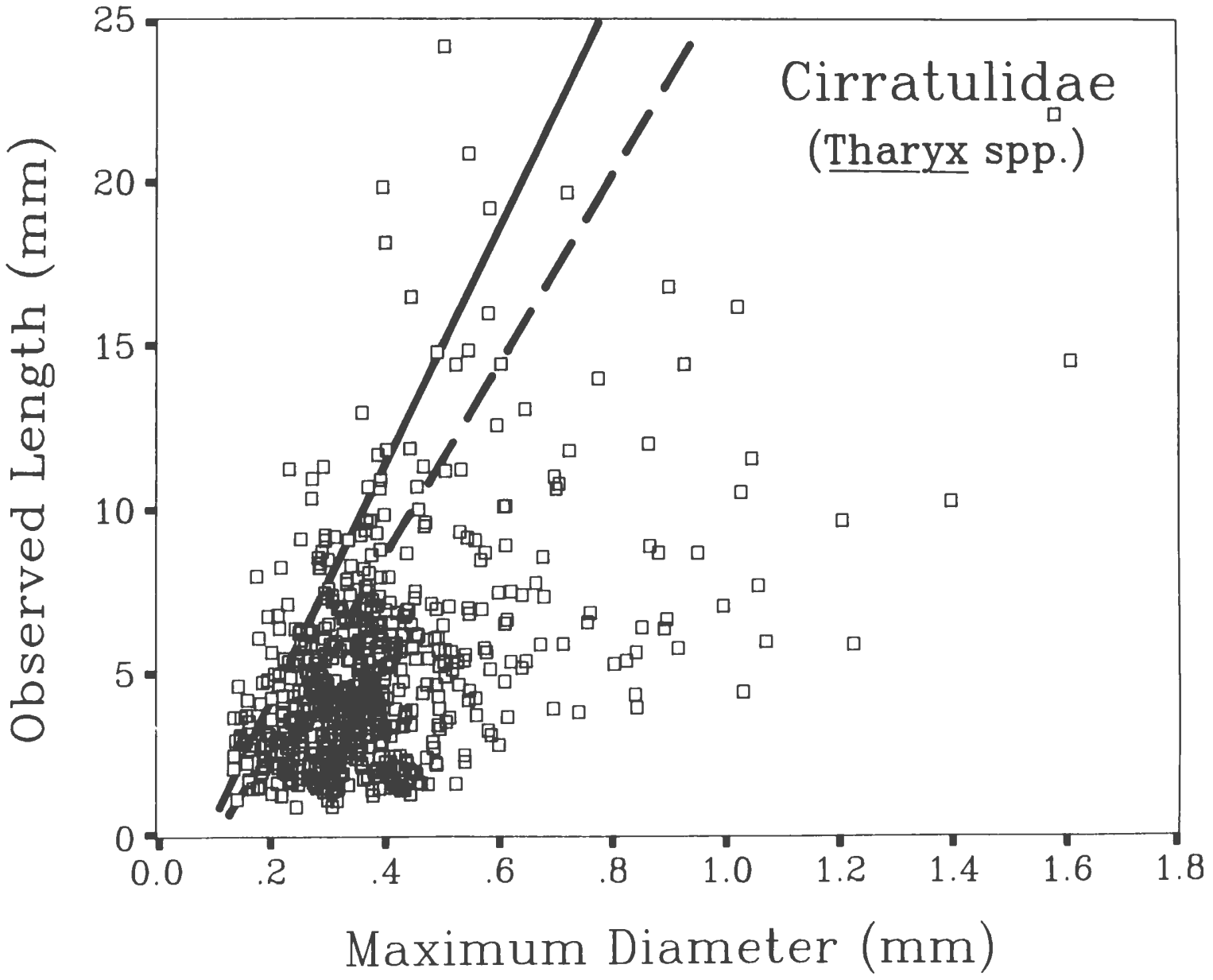

Apistobranchidae
Observed Length (mm)
Maximum Diameter (mm)
0
2
4
6
8
10
12
14
16
18
20
22
24
26
.2
.4
.6
.8
1.0
1.2
1.4
1.6
1.8

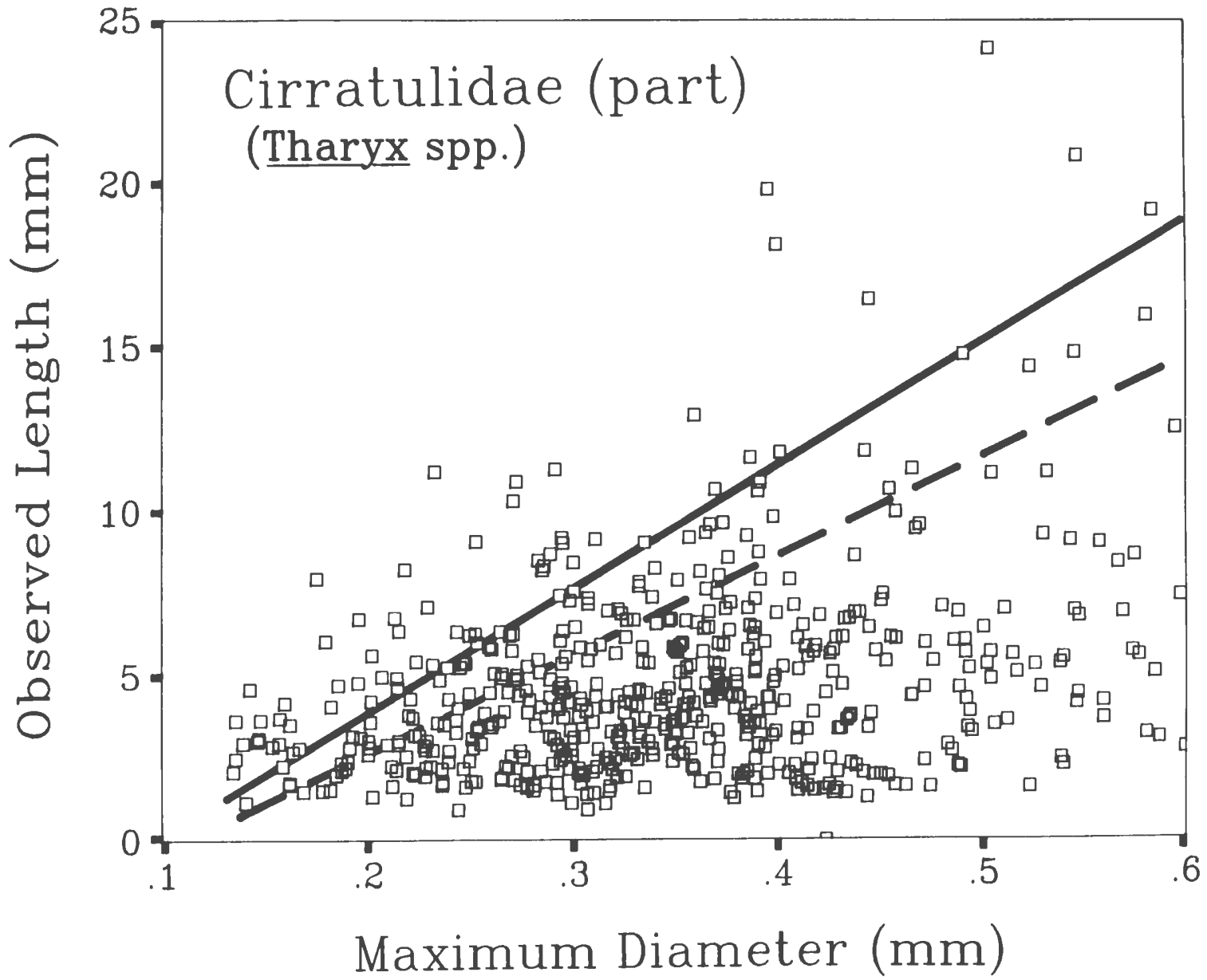

Capitellidae
Observed Length (mm)
Maximum Diameter (mm)
0
10
20
30
40
0.0
.2
.4
.6
.8
1.0
1.2
1.4
1.6
1.8
2.0
2.2

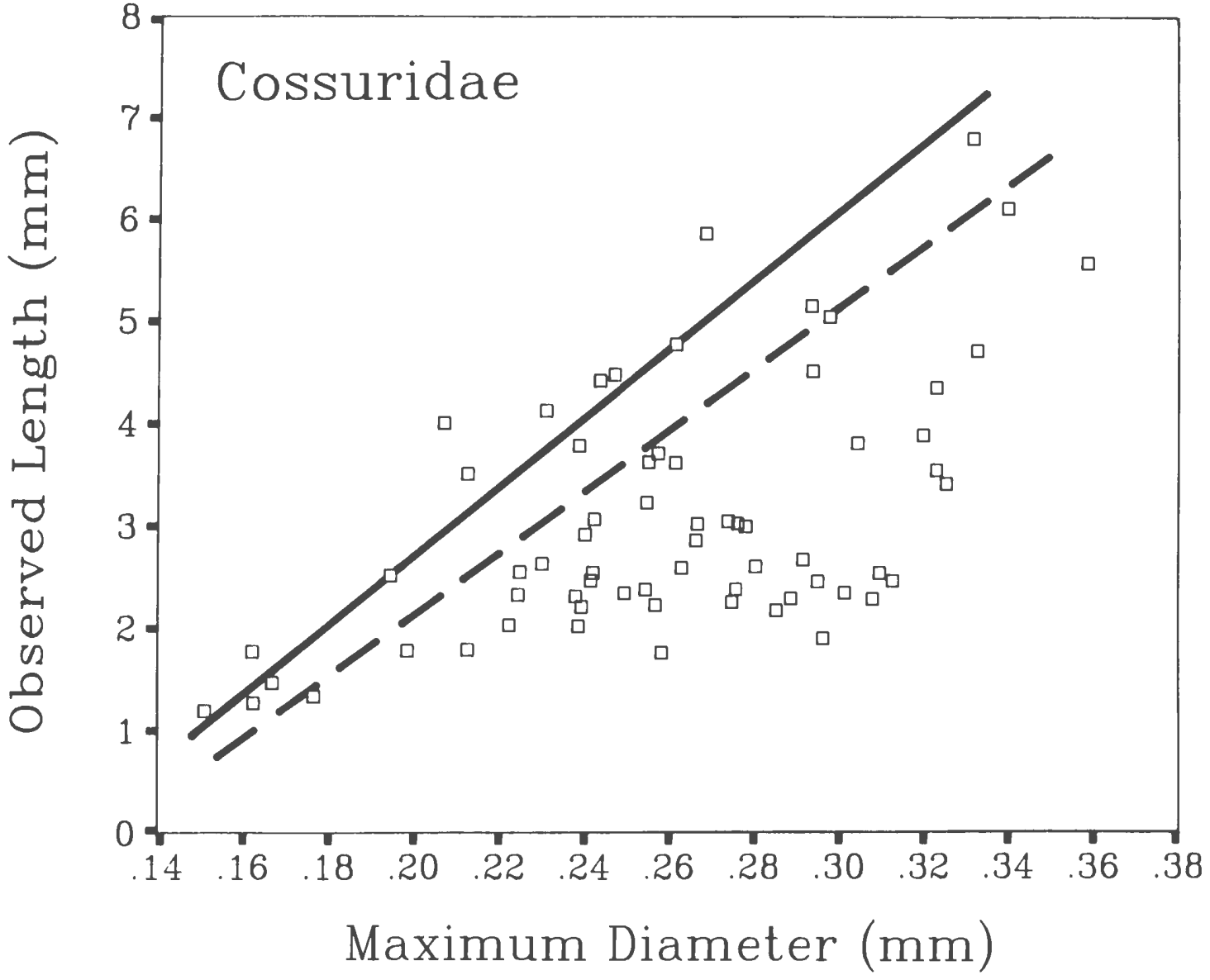

Cirratulidae
(Cirratulus spp.)
Observed Length (mm)
16
14
12
10
8
6
4
2
.2
.3
.4
.5
.6
.7
.8
.9
1.0
Maximum Diameter (mm)

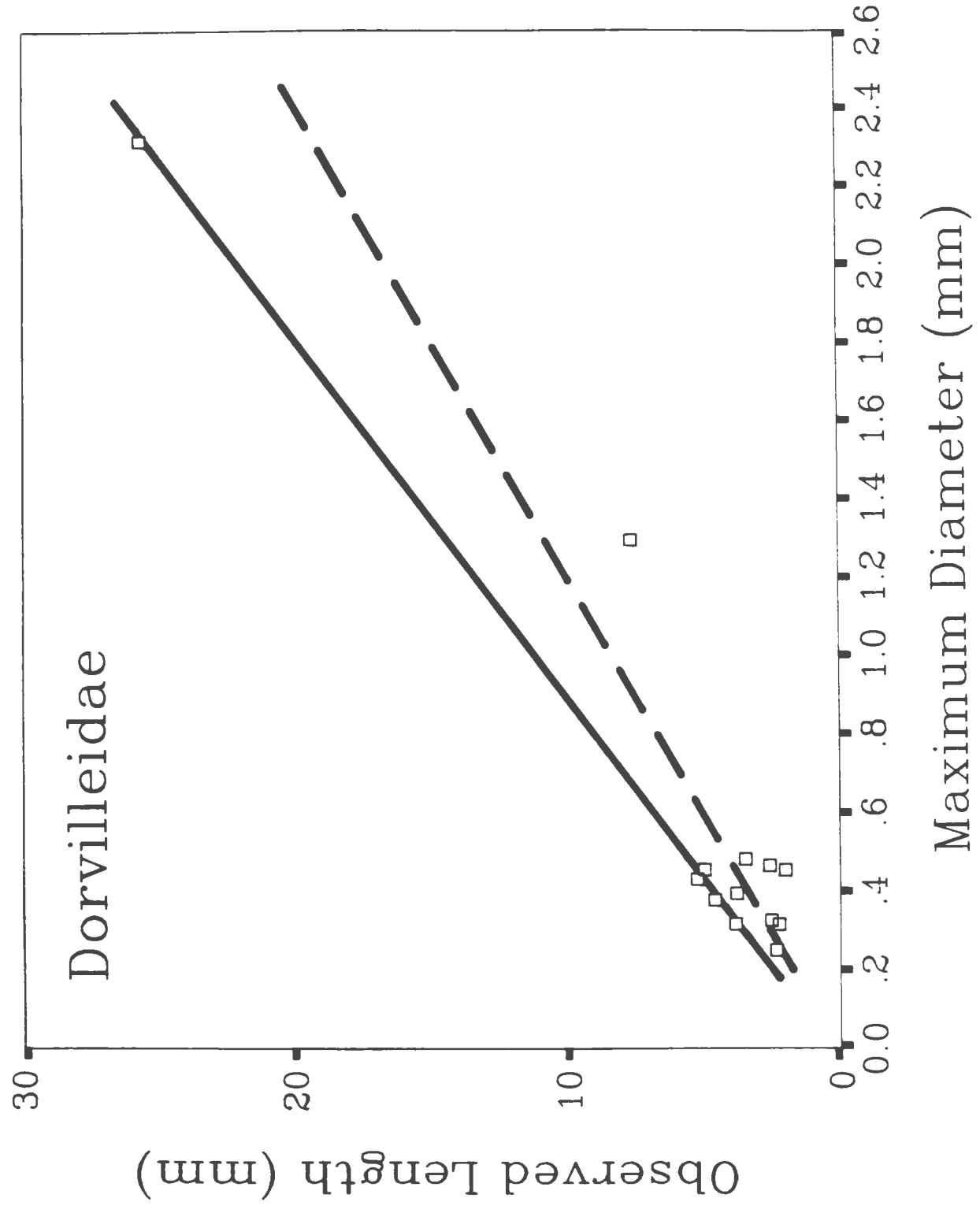

Cirratulidae
(Chaetozone sp.)
Observed Length (mm)
Maximum Diameter (mm)
0
5
10
15
20
25
0.0
.2
.4
.6
.8
1.0
1.2
1.4
1.6

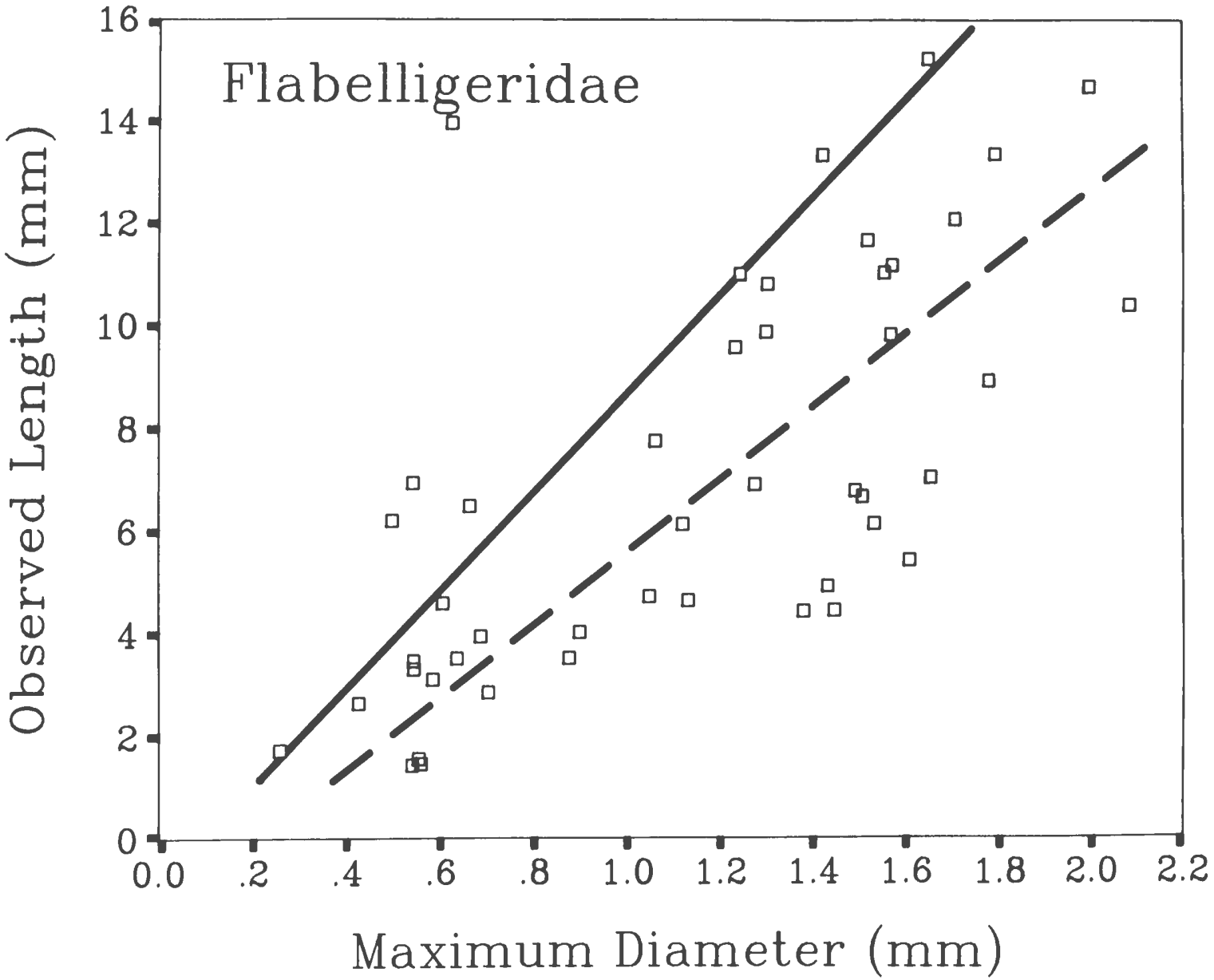

Cirratulidae
(Dodecaceria spp.)
Observed Length (mm)
Maximum Diameter (mm)
0
2
4
6
8
10
12
14
16
18
20
.1
.2
.3
.4
.5
.6
.7
.8
.9
1.0
1.1

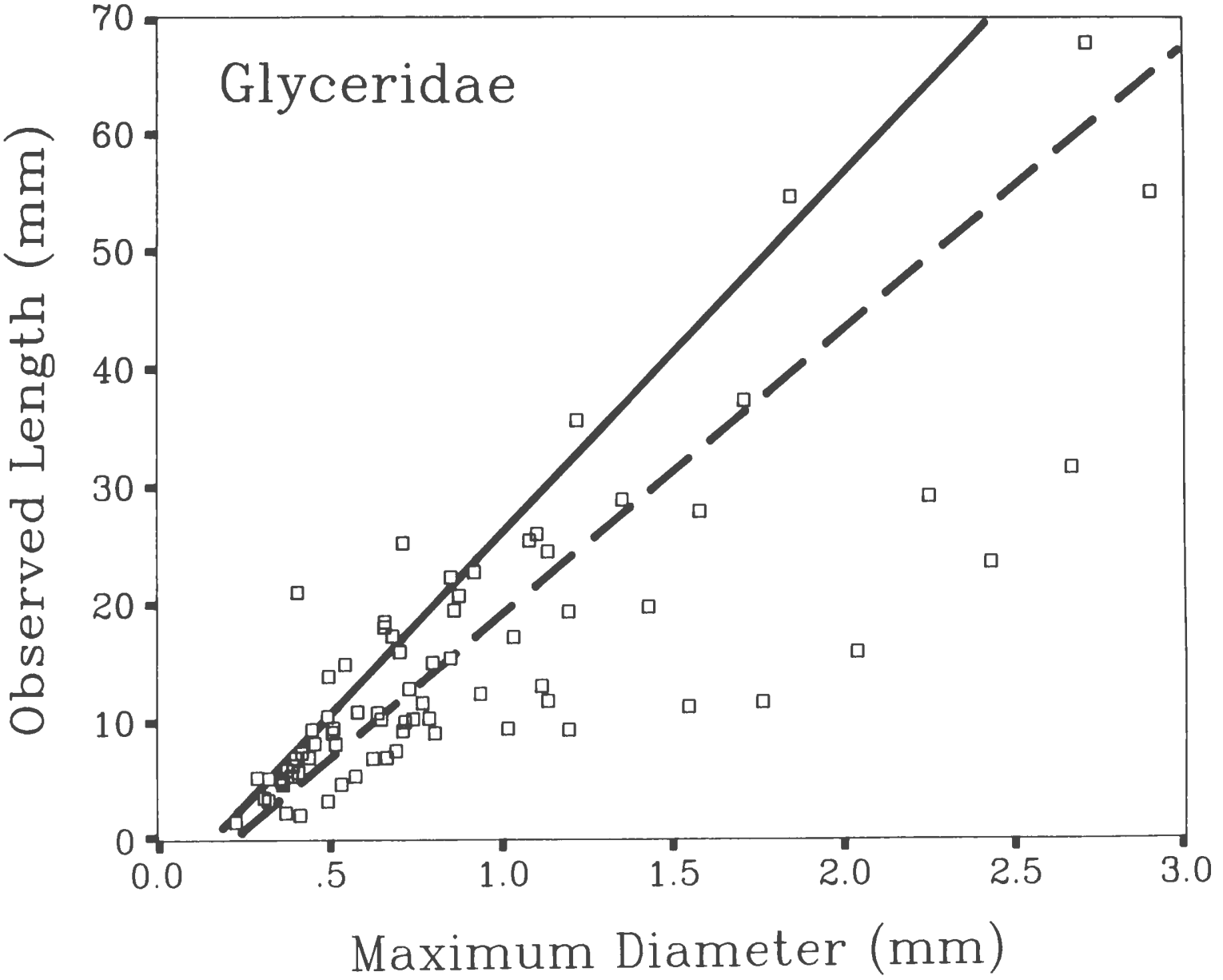

Cirratulidae
(Tharyx spp.)
Observed Length (mm)
Maximum Diameter (mm)
0
5
10
15
20
25
0.0
.2
.4
.6
.8
1.0
1.2
1.4
1.6
1.8

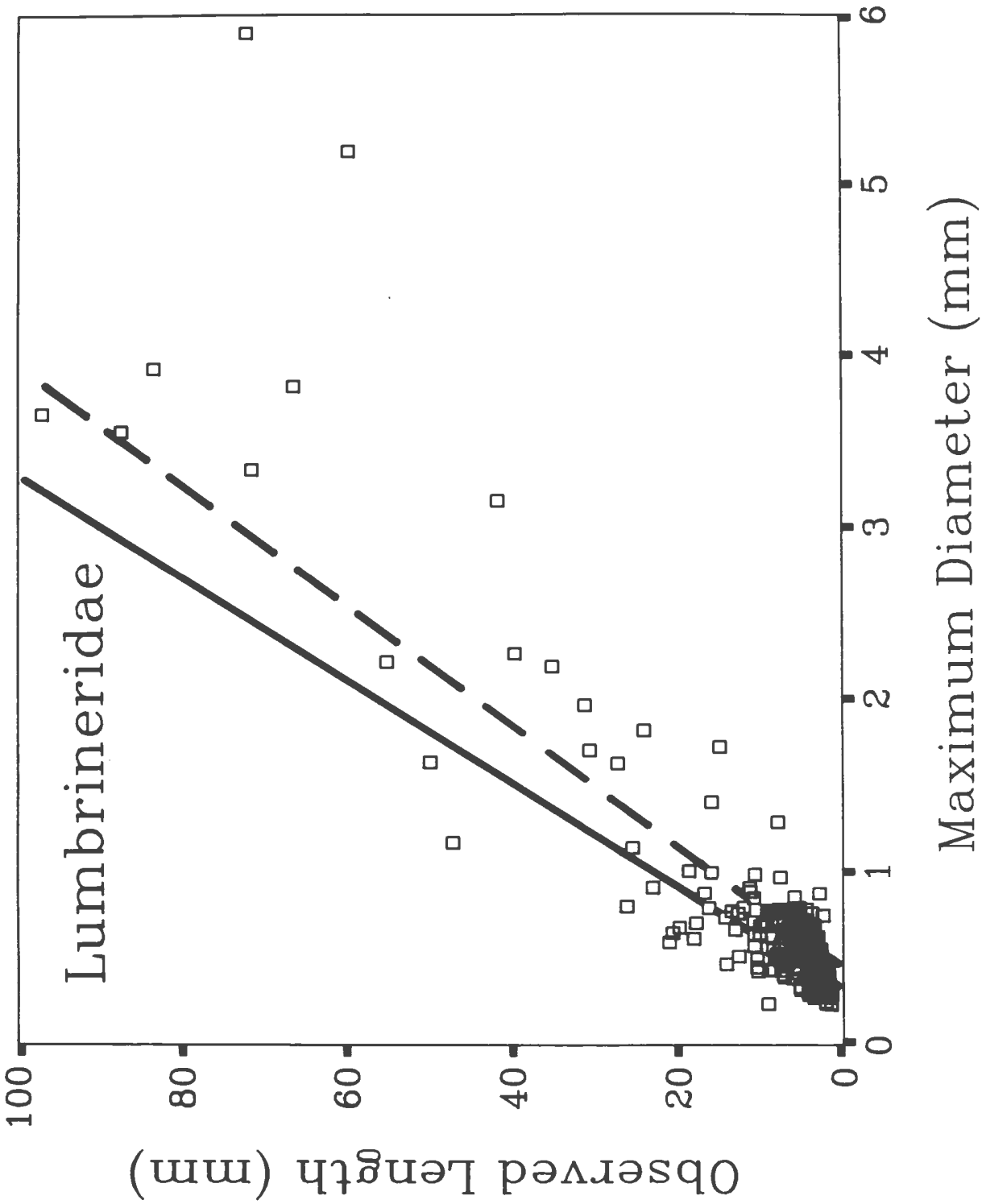

Cirratulidae (part)
(Tharyx spp.)
Observed Length (mm)
25
20
15
10
5
0
.1
.2
.3
.4
.5
.6
Maximum Diameter (mm)

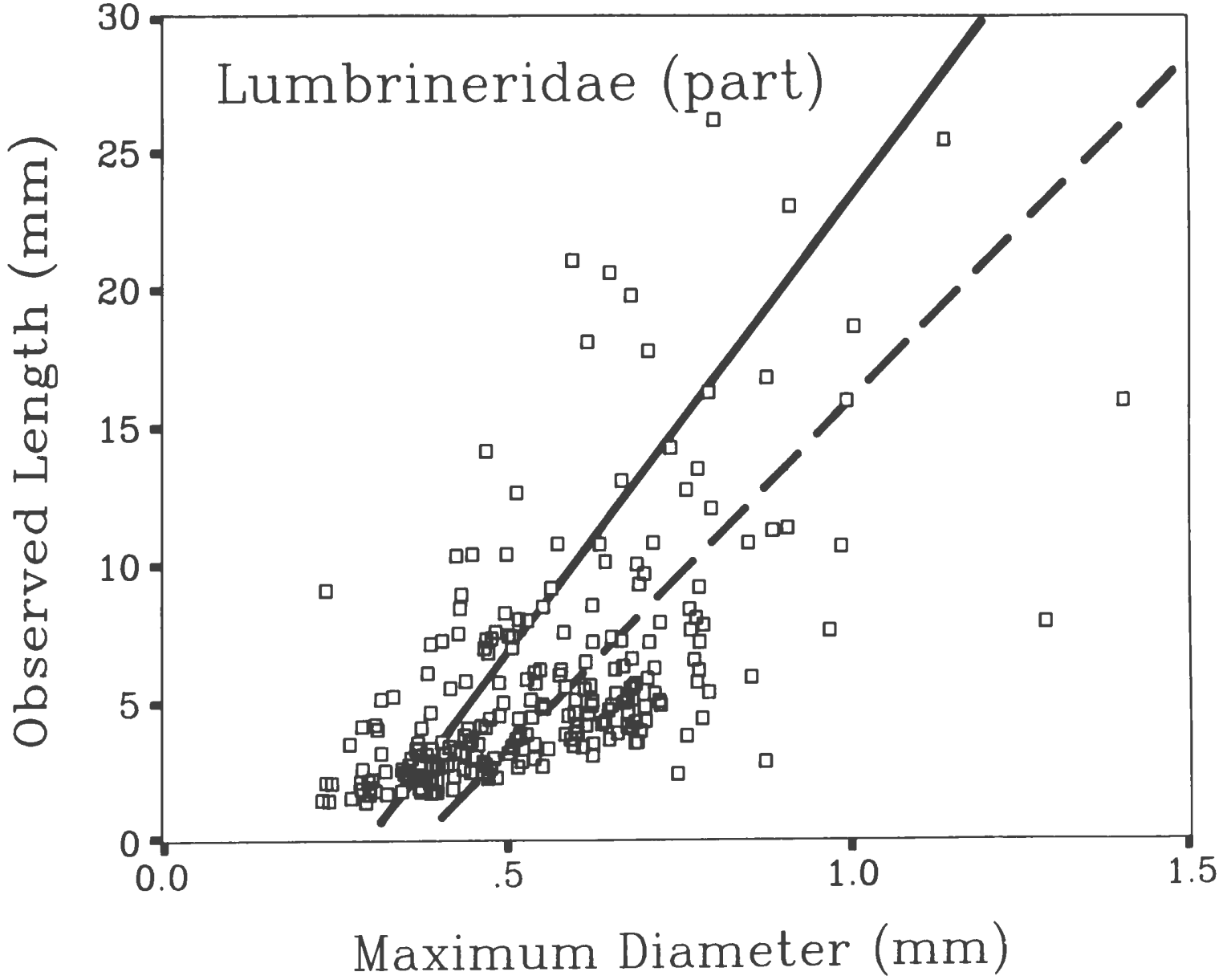

Cossuridae
Observed Length (mm)
Maximum Diameter (mm)
0
1
2
3
4
5
6
7
8
.14
.16
.18
.20
.22
.24
.26
.28
.30
.32
.34
.36
.38

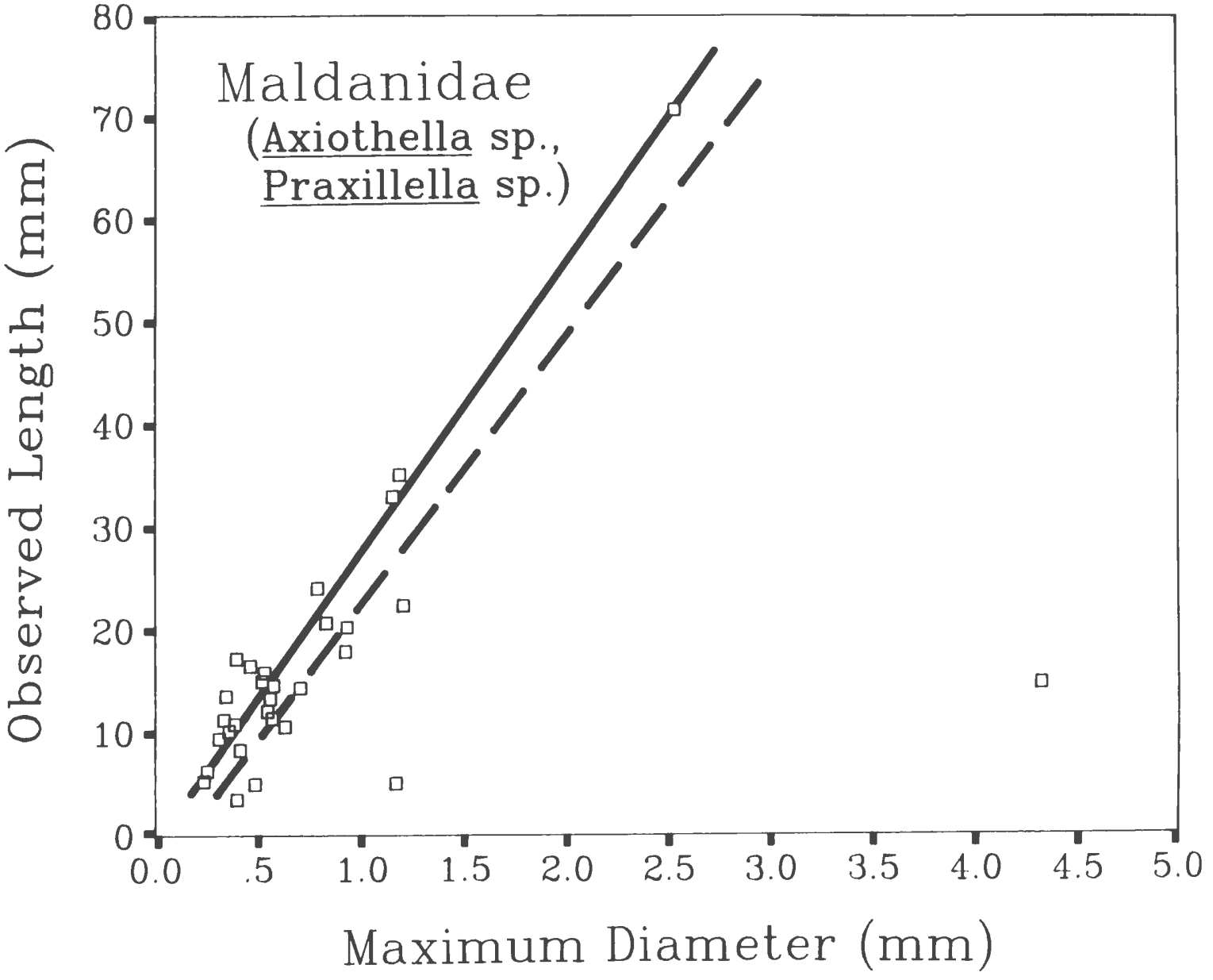

Dorvilleidae
Observed Length (mm)
Maximum Diameter (mm)
0
10
20
30
0.0
.2
.4
.6
.8
1.0
1.2
1.4
1.6
1.8
2.0
2.2
2.4
2.6

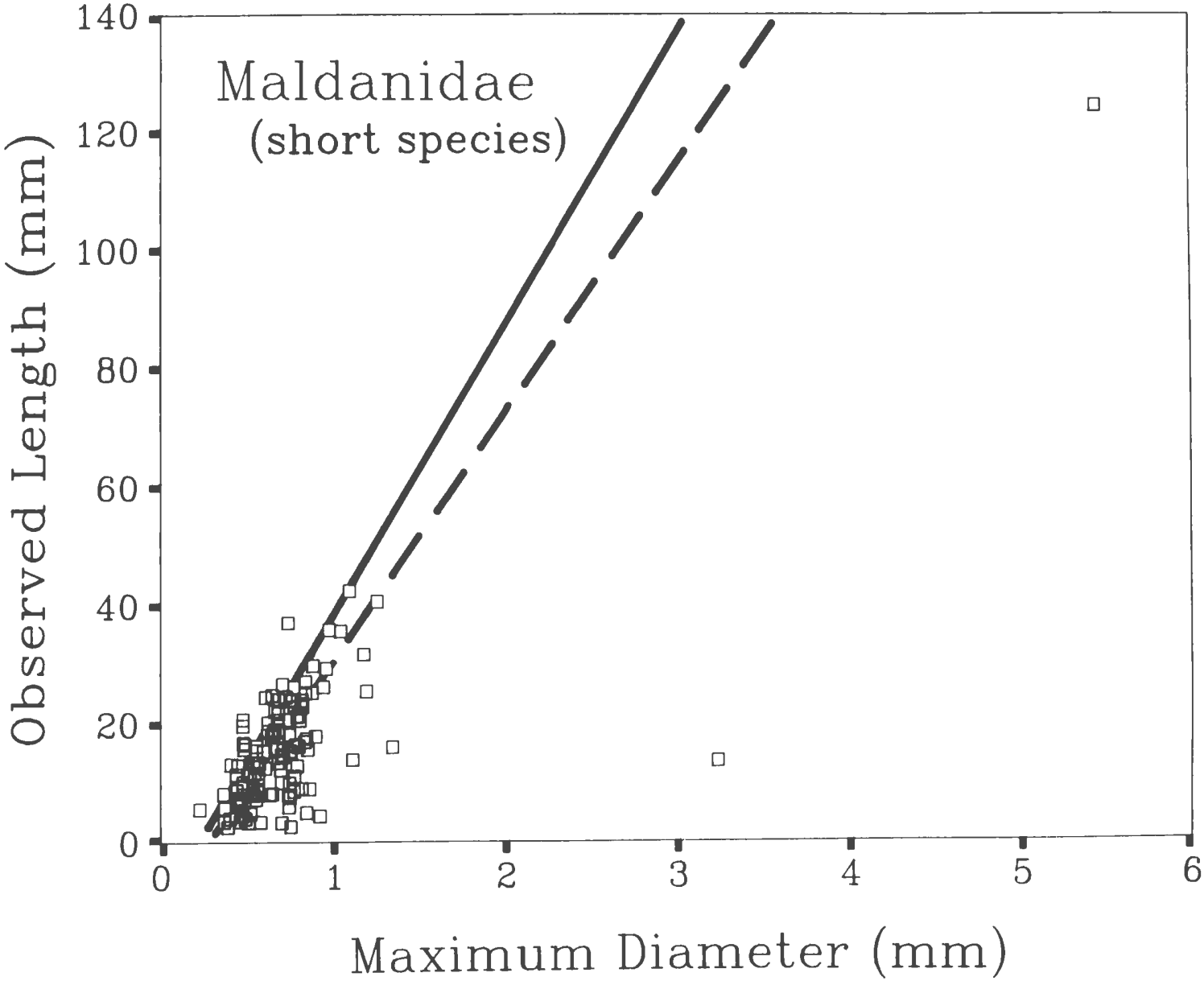

Flabelligeridae
Observed Length (mm)
Maximum Diameter (mm)
0
2
4
6
8
10
12
14
16
0.0
.2
.4
.6
.8
1.0
1.2
1.4
1.6
1.8
2.0
2.2

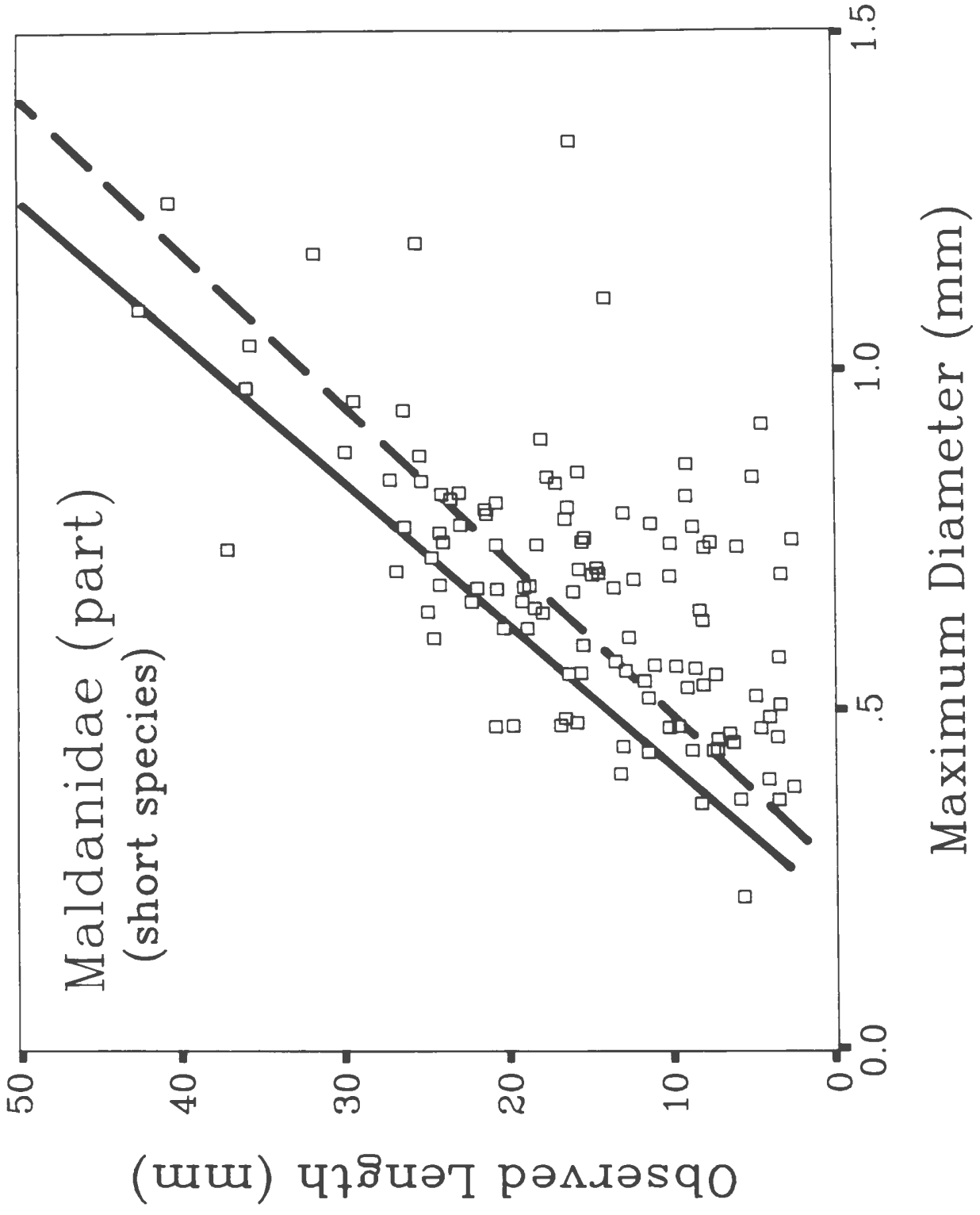

Glyceridae
Observed Length (mm)
Maximum Diameter (mm)
0
10
20
30
40
50
60
70
0.0
.5
1.0
1.5
2.0
2.5
3.0

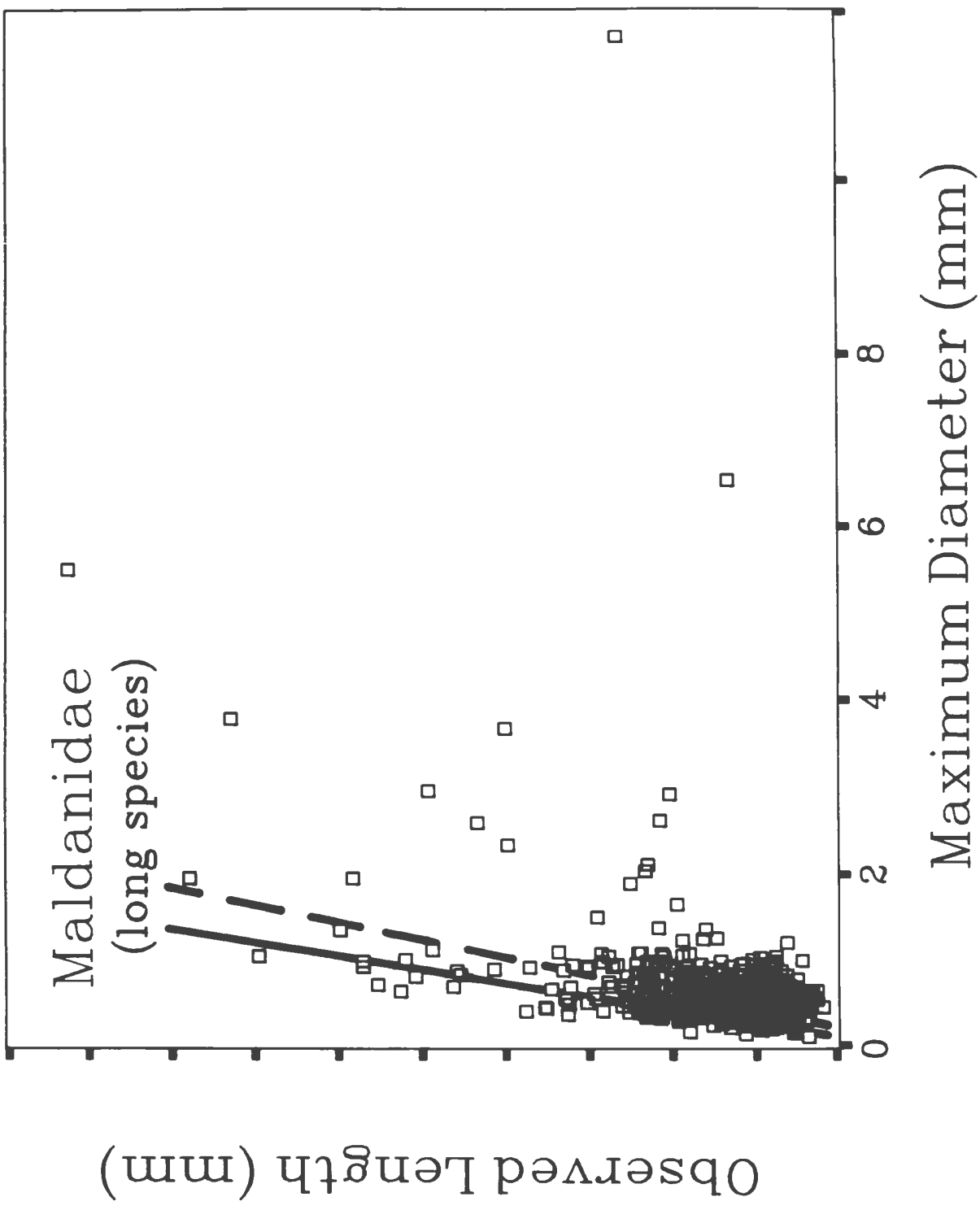

Lumbrineridae
Observed Length (mm)
Maximum Diameter (mm)
0
20
40
60
80
100
0
1
2
3
4
5
6

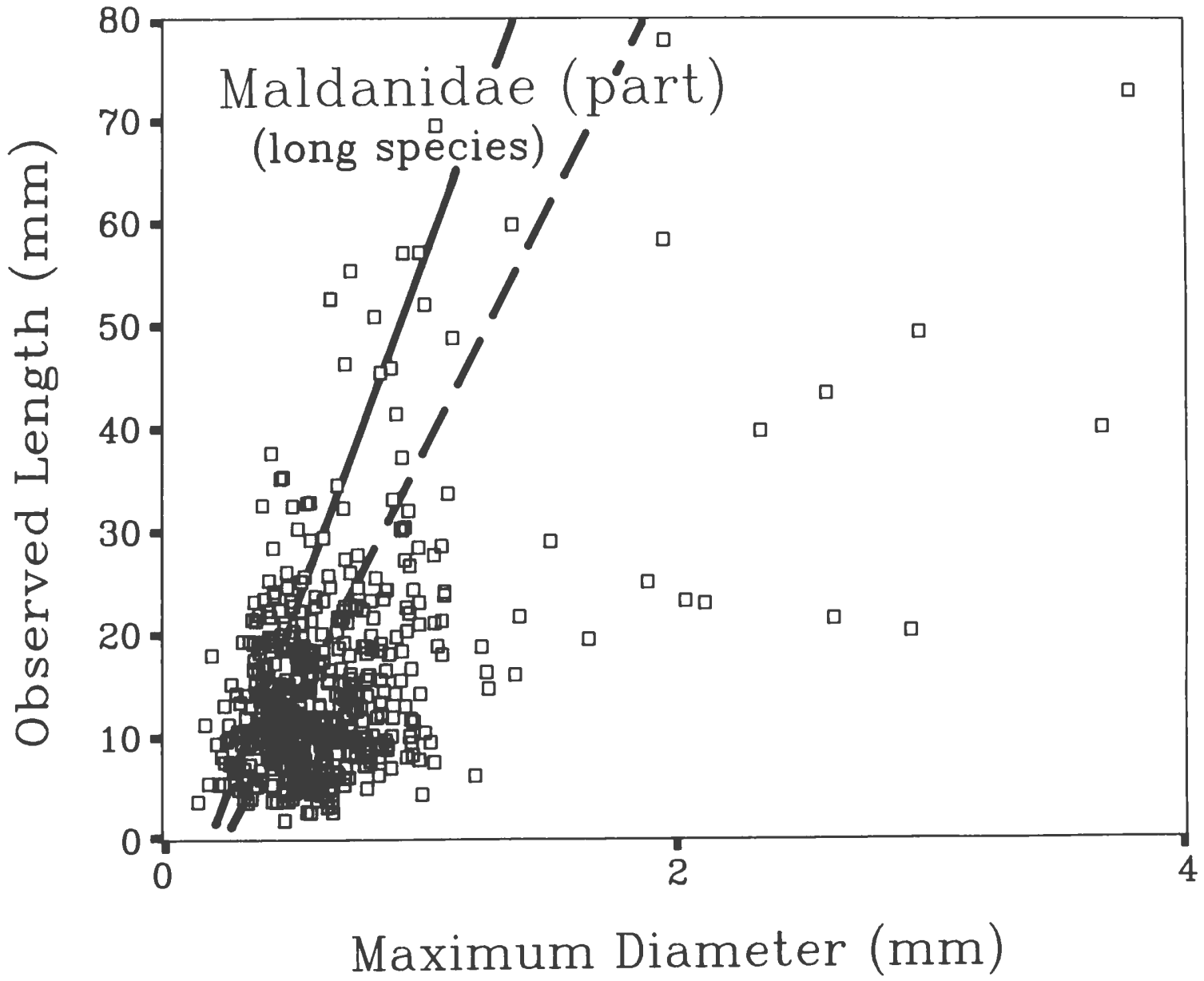

Lumbrineridae (part)
Observed Length (mm)
Maximum Diameter (mm)
0
5
10
15
20
25
30
0.0
.5
1.0
1.5

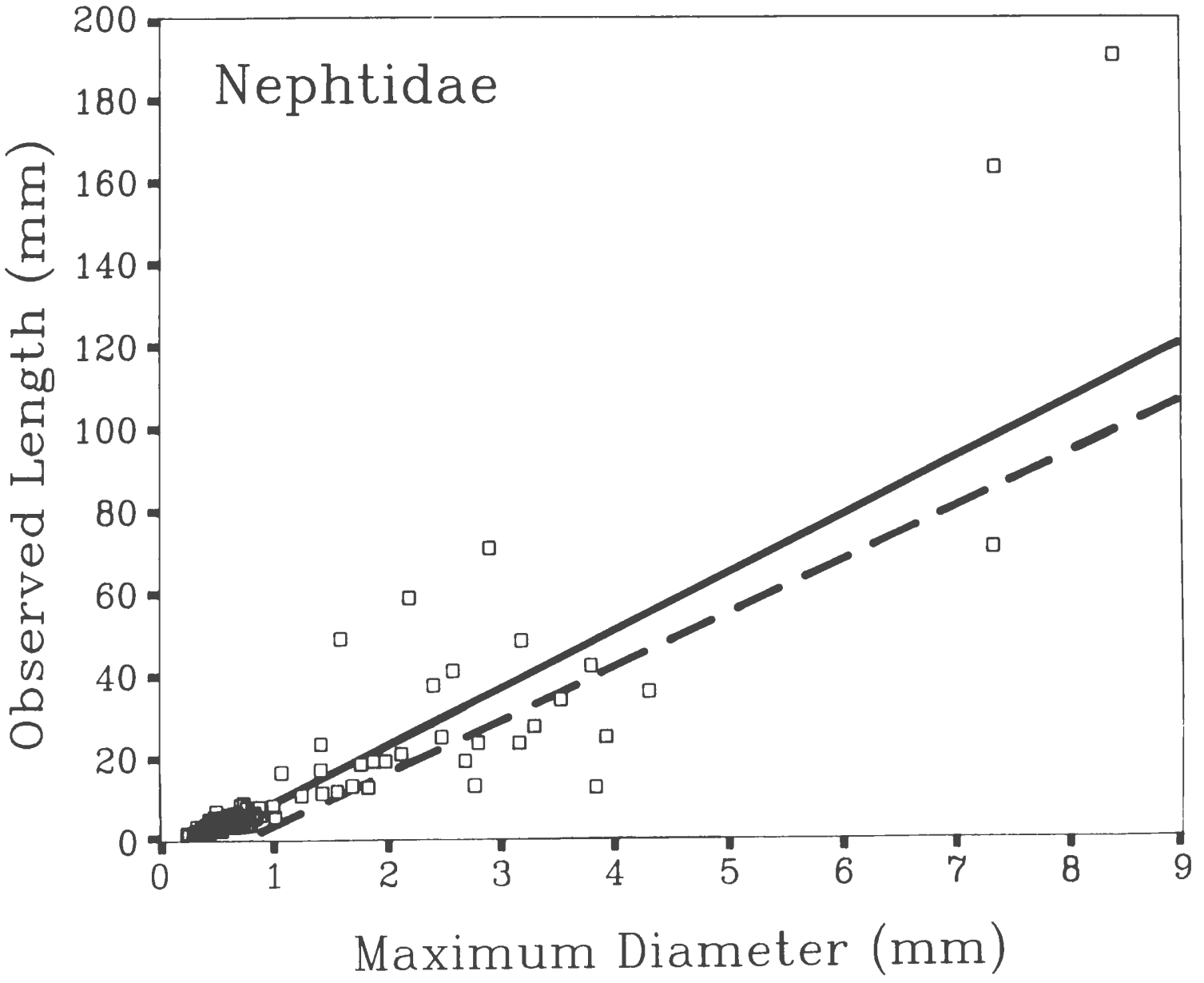

Maldanidae
(Axiothella sp.,
Praxillella sp.)
Observed Length (mm)
Maximum Diameter (mm)
0
10
20
30
40
50
60
70
80
0.0
.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0
4.5
5.0

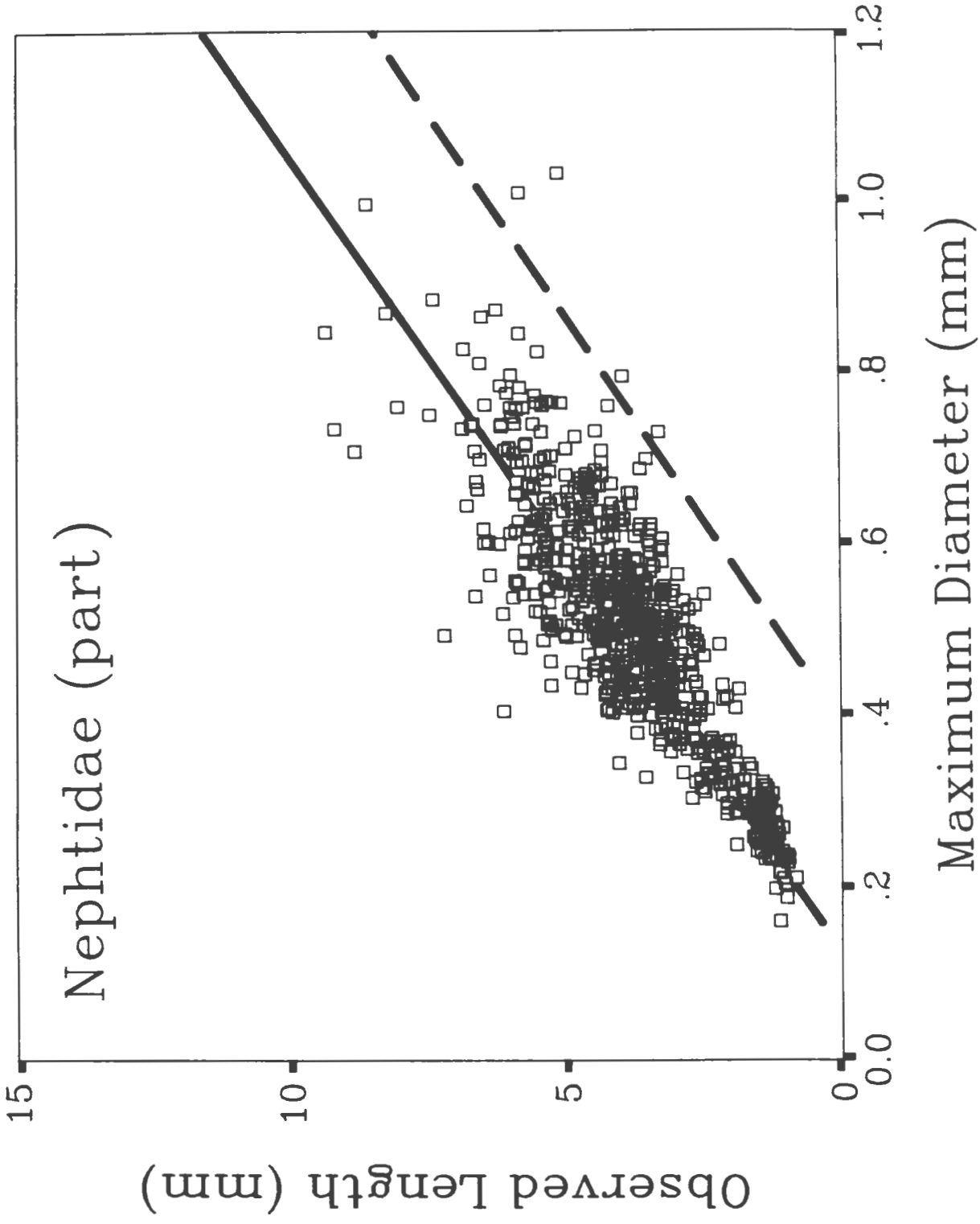

Maldanidae
(short species)
Observed Length (mm)
Maximum Diameter (mm)
0
20
40
60
80
100
120
140
0
1
2
3
4
5
6

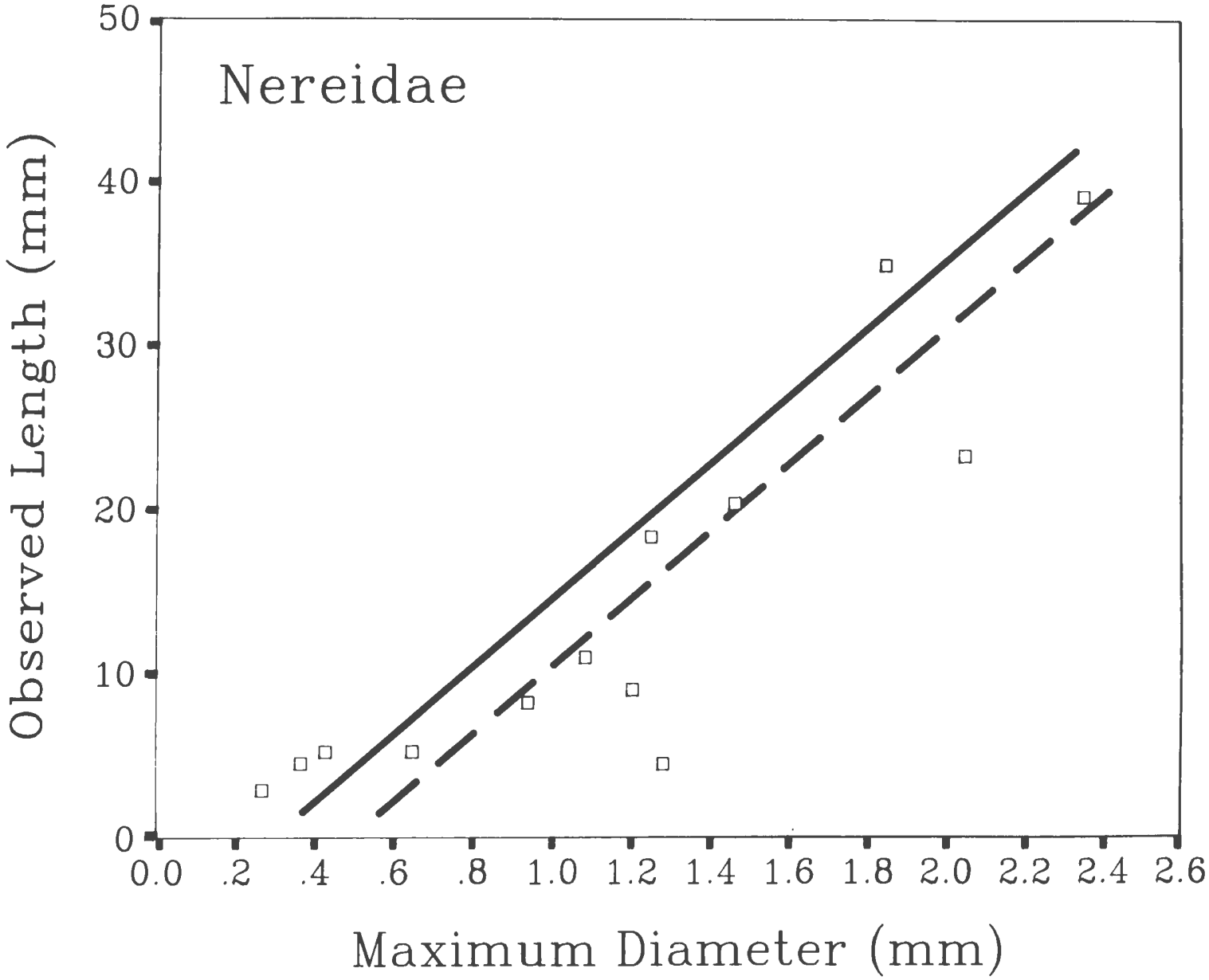

Maldanidae (part)
(short species)
Observed Length (mm)
Maximum Diameter (mm)
0
10
20
30
40
50
0.0
.5
1.0
1.5

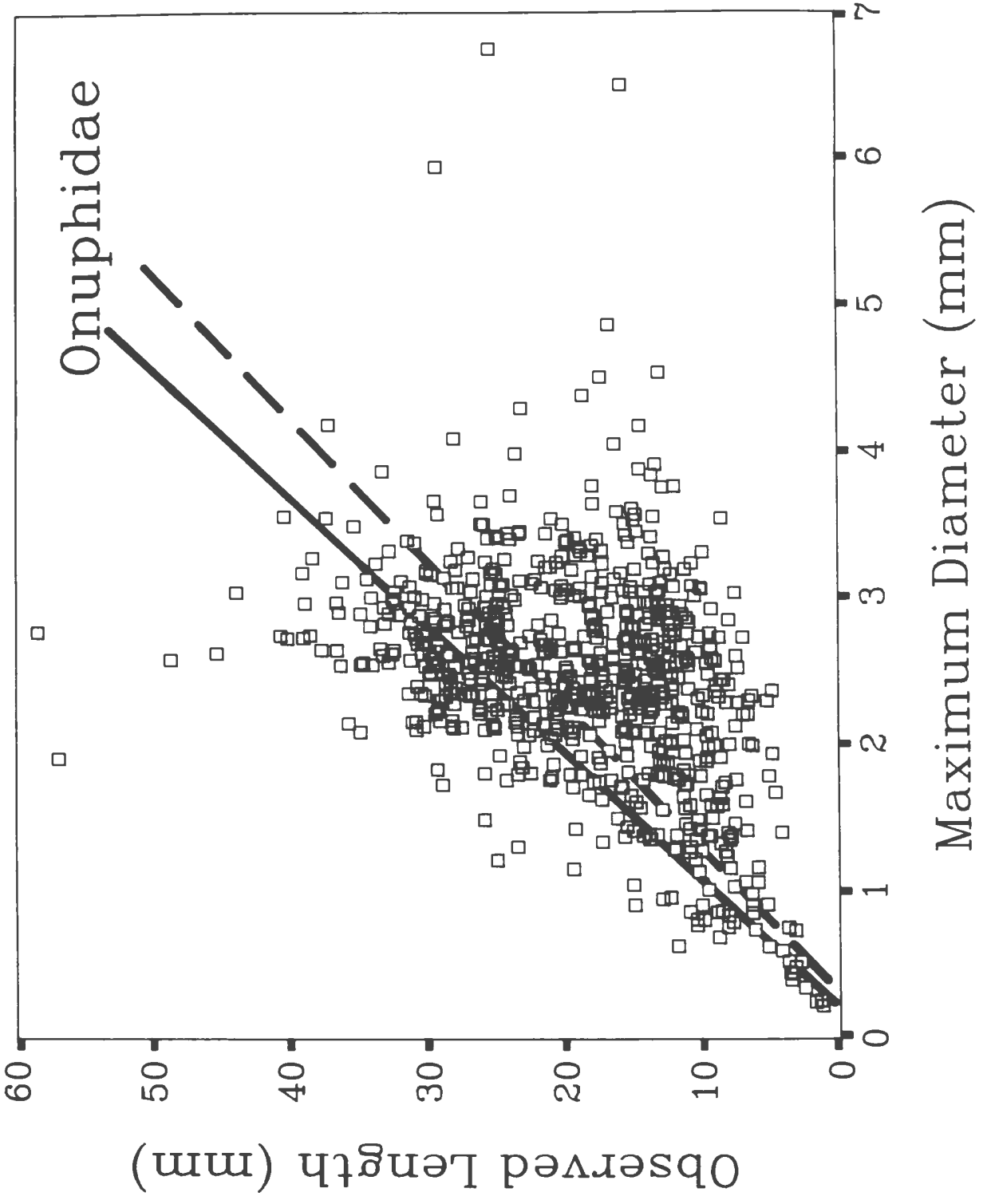

Maldanidae
(long species)
Observed Length (mm)
Maximum Diameter (mm)
0
2
4
6
8

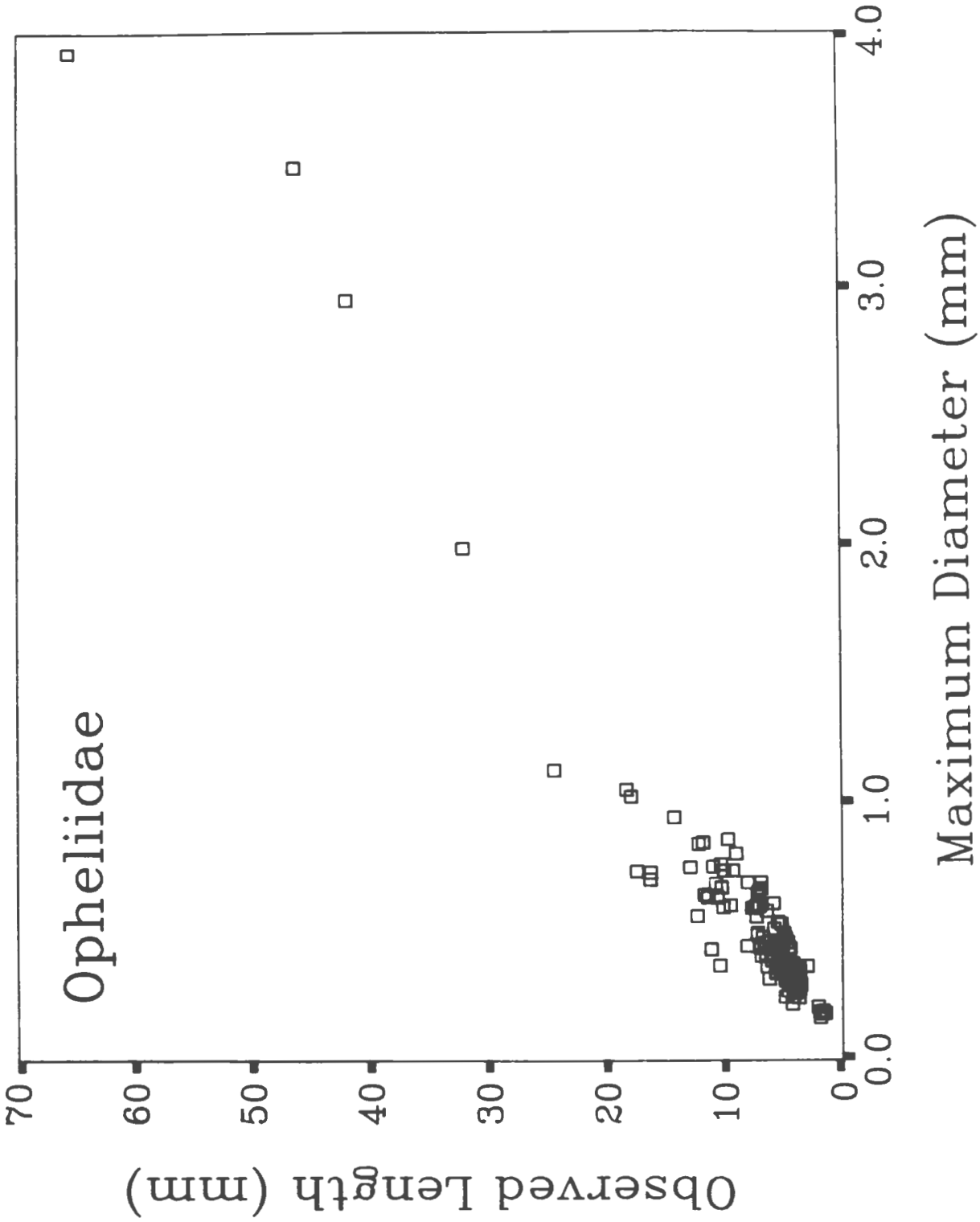

Maldanidae (part)
(long species)
Observed Length (mm)
Maximum Diameter (mm)
0
10
20
30
40
50
60
70
80
0
2
4

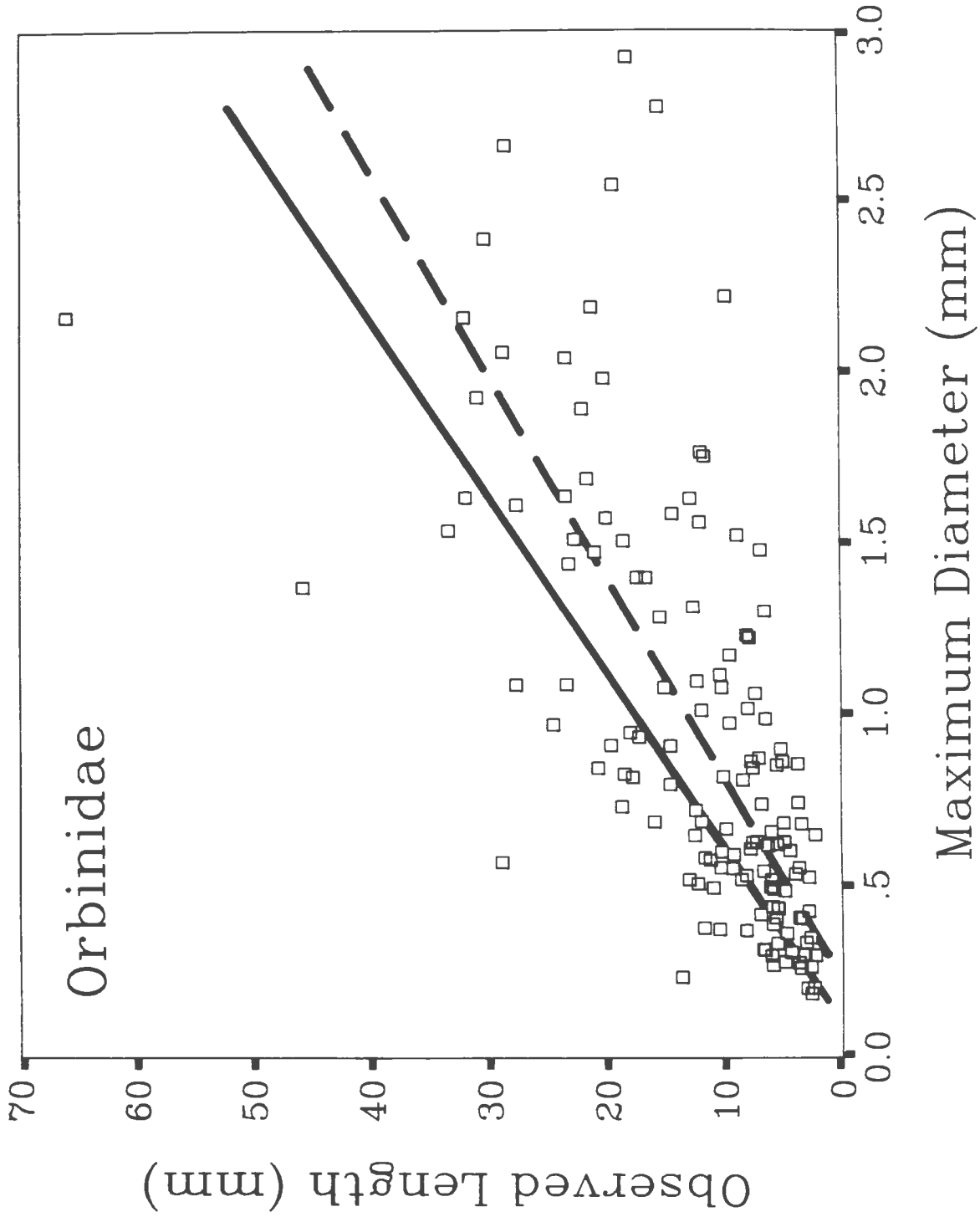

Nephtidae
Observed Length (mm)
Maximum Diameter (mm)
0
20
40
60
80
100
120
140
160
180
200
0
1
2
3
4
5
6
7
8
9

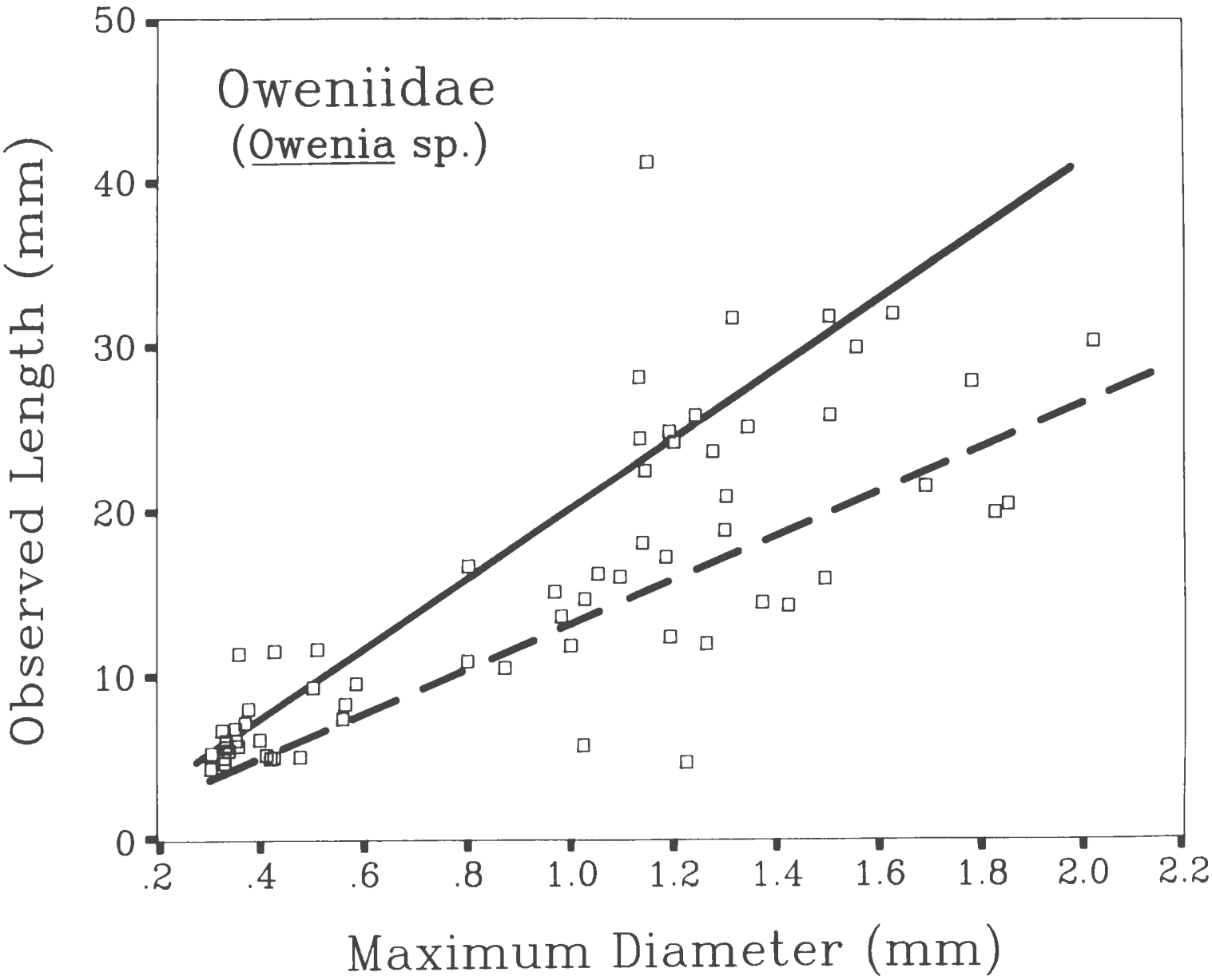

Nephtidae (part)
Observed Length (mm)
Maximum Diameter (mm)
0
5
10
15
0.0
.2
.4
.6
.8
1.0
1.2

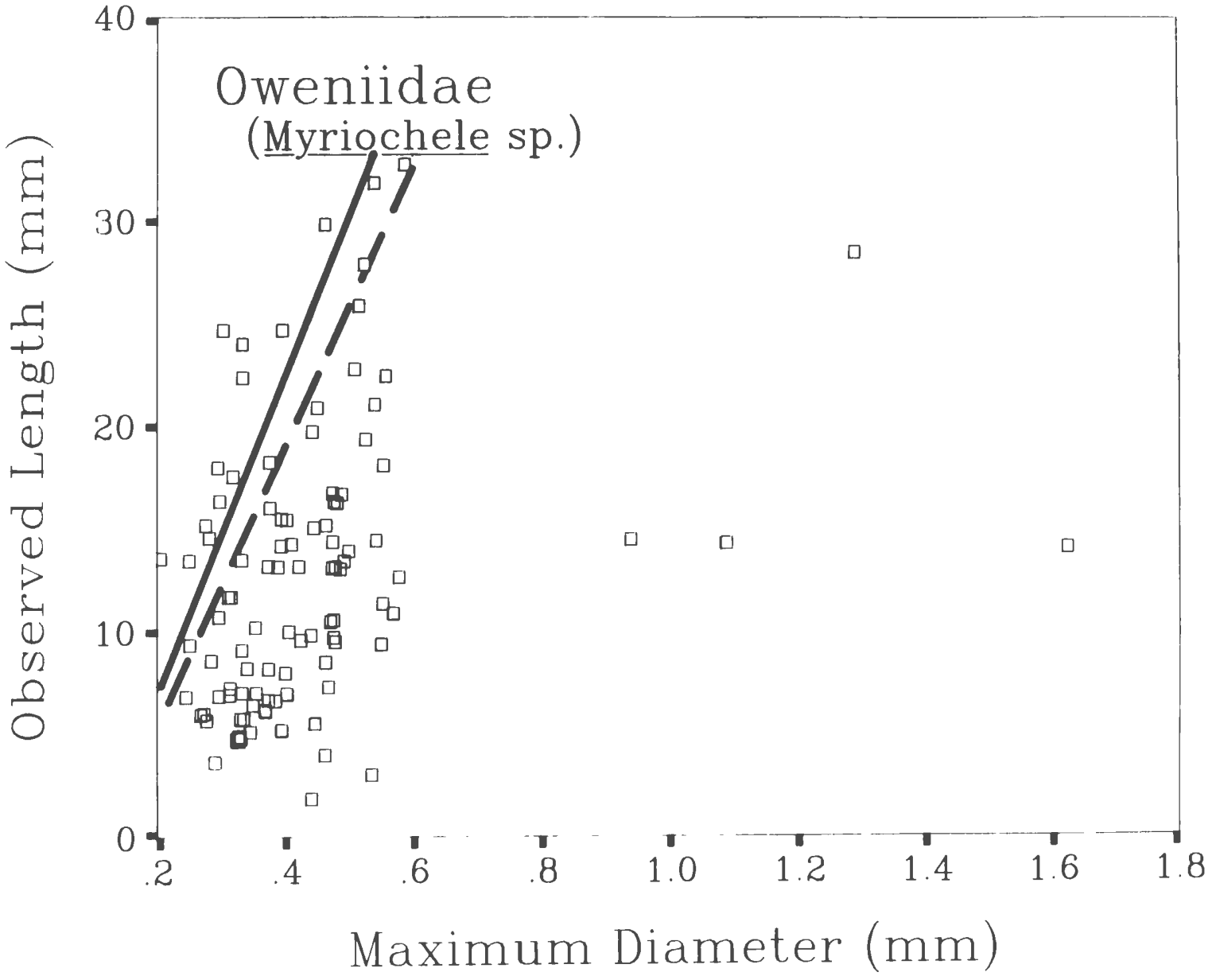

Nereidae
Observed Length (mm)
50
40
30
20
10
0
0.0
.2
.4
.6
.8
1.0
1.2
1.4
1.6
1.8
2.0
2.2
2.4
2.6
Maximum Diameter (mm)

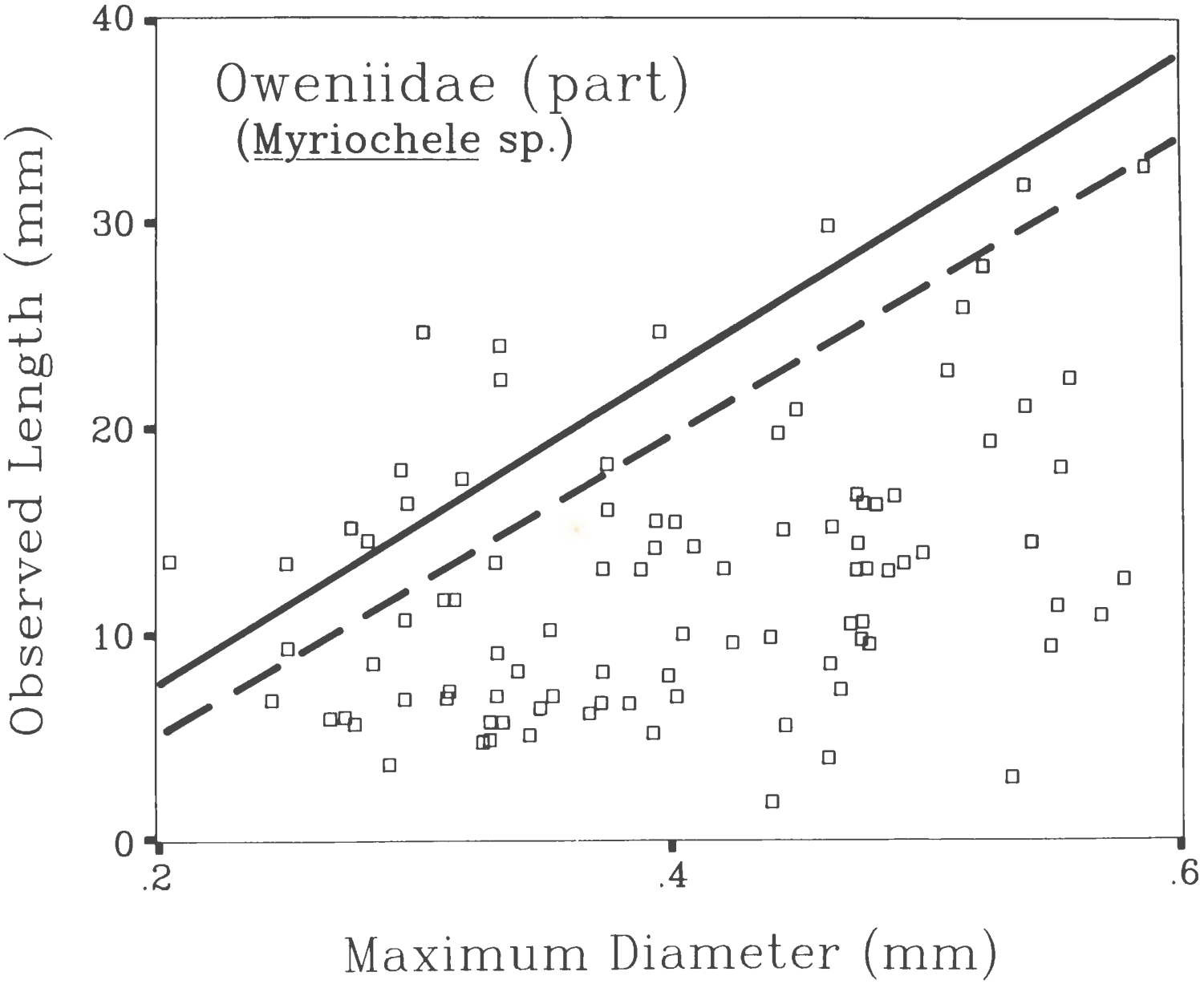

Onuphidae
Observed Length (mm)
Maximum Diameter (mm)
0
10
20
30
40
50
60
0
1
2
3
4
5
6
7

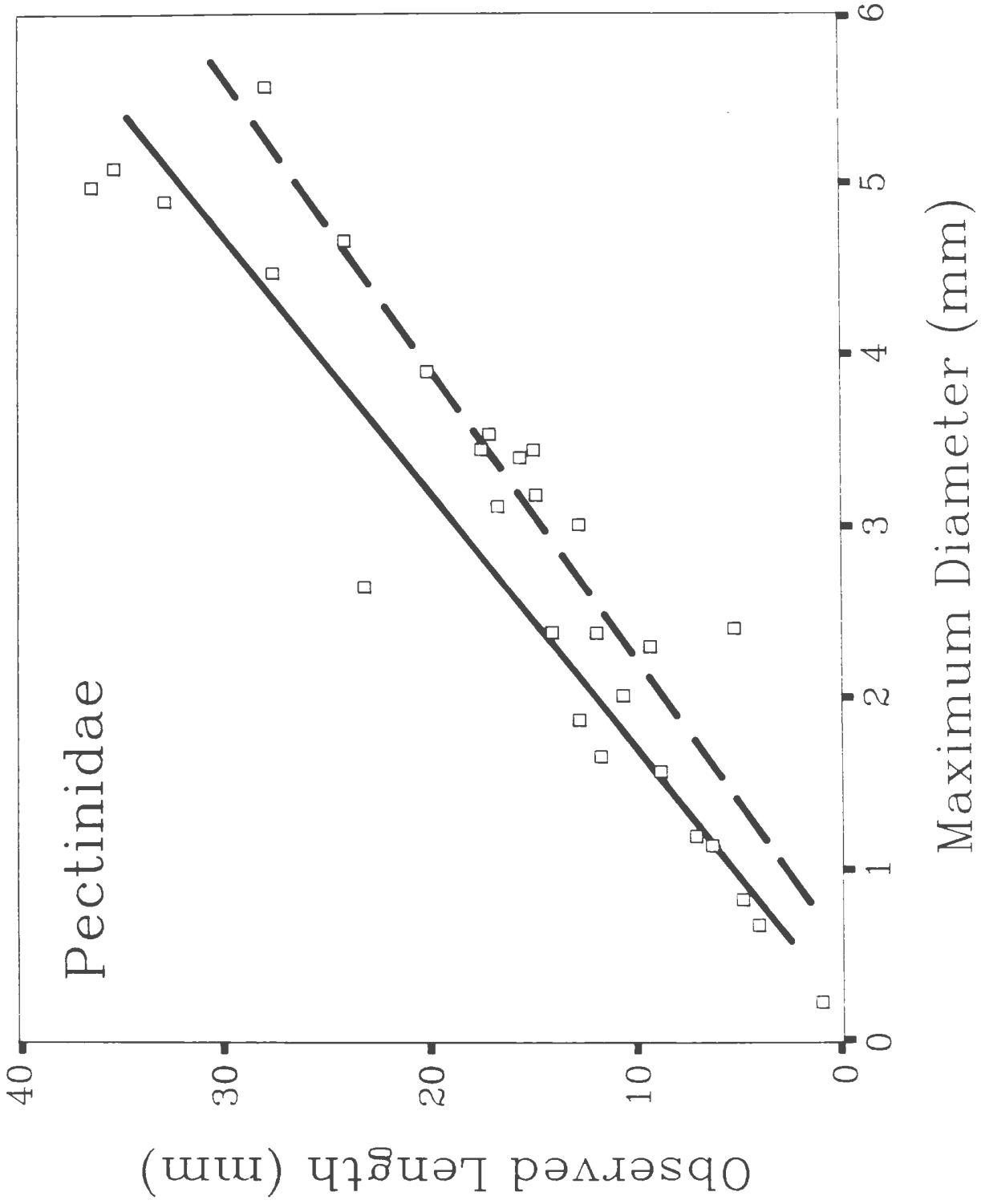

Ophelidae
Observed Length (mm)
Maximum Diameter (mm)
0
10
20
30
40
50
60
70
0.0
1.0
2.0
3.0
4.0

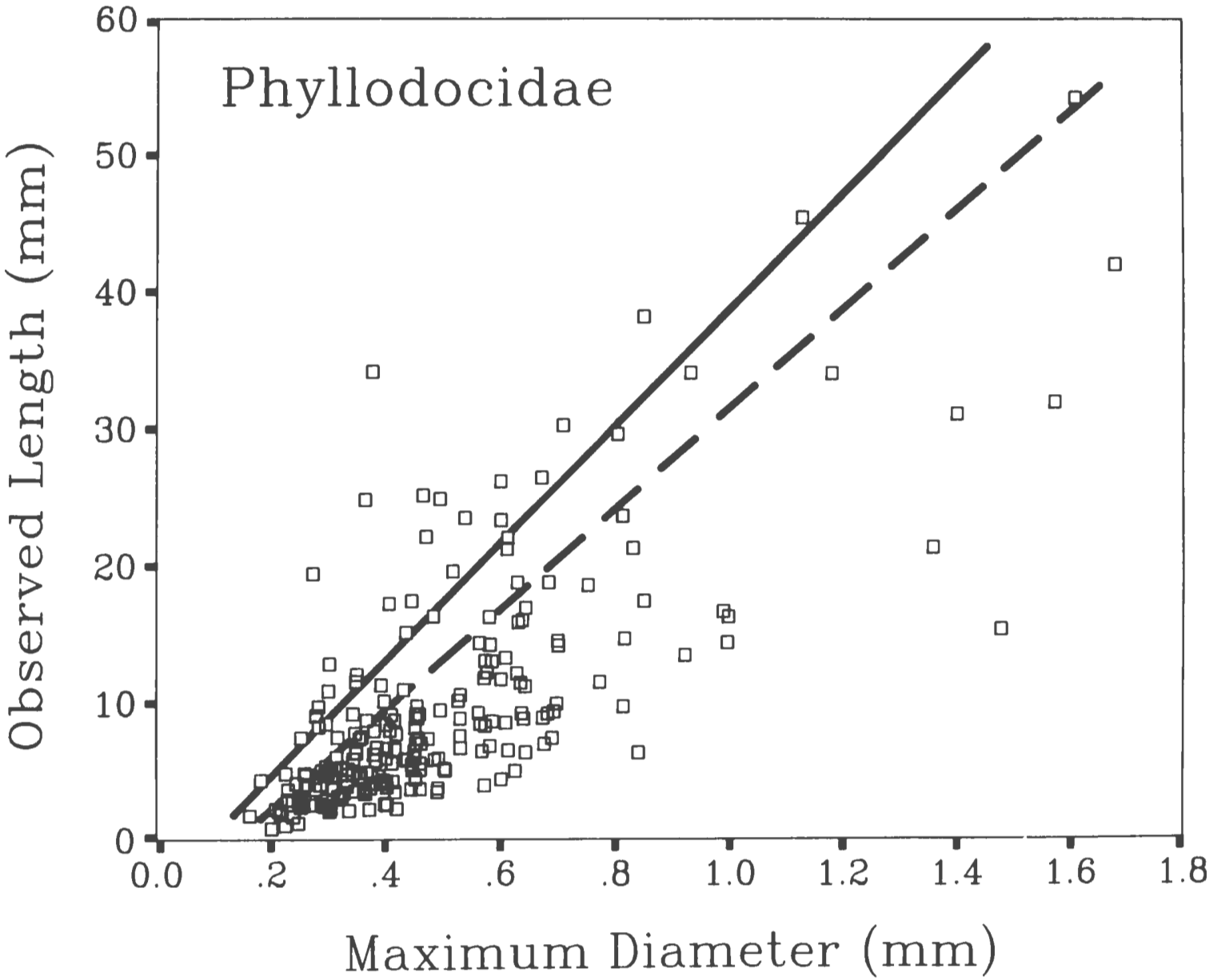

Orbinidae
Observed Length (mm)
Maximum Diameter (mm)
0
10
20
30
40
50
60
70
0.0
.5
1.0
1.5
2.0
2.5
3.0

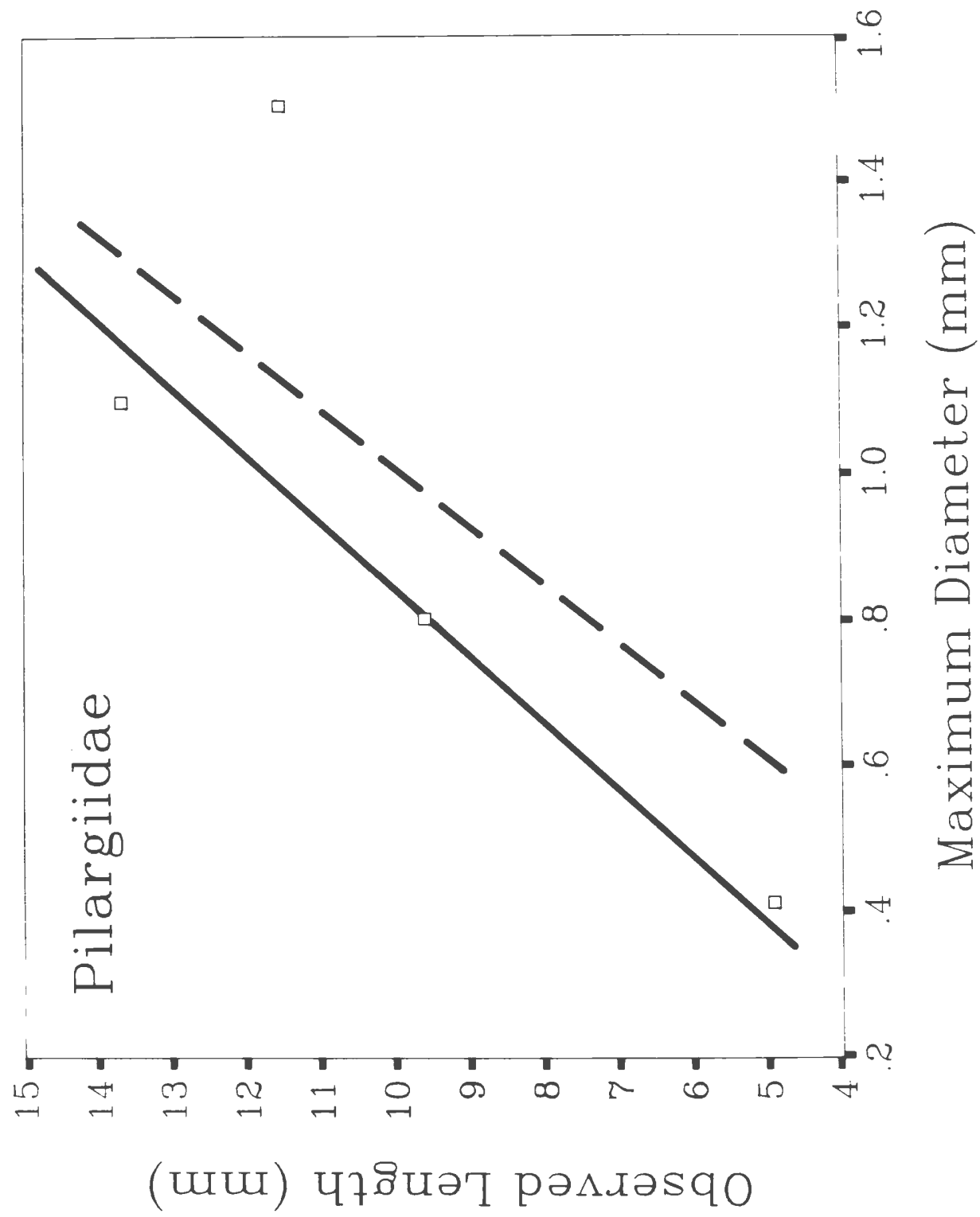

Oweniidae
(Owenia sp.)
Observed Length (mm)
Maximum Diameter (mm)
0
10
20
30
40
50
.2
.4
.6
.8
1.0
1.2
1.4
1.6
1.8
2.0
2.2

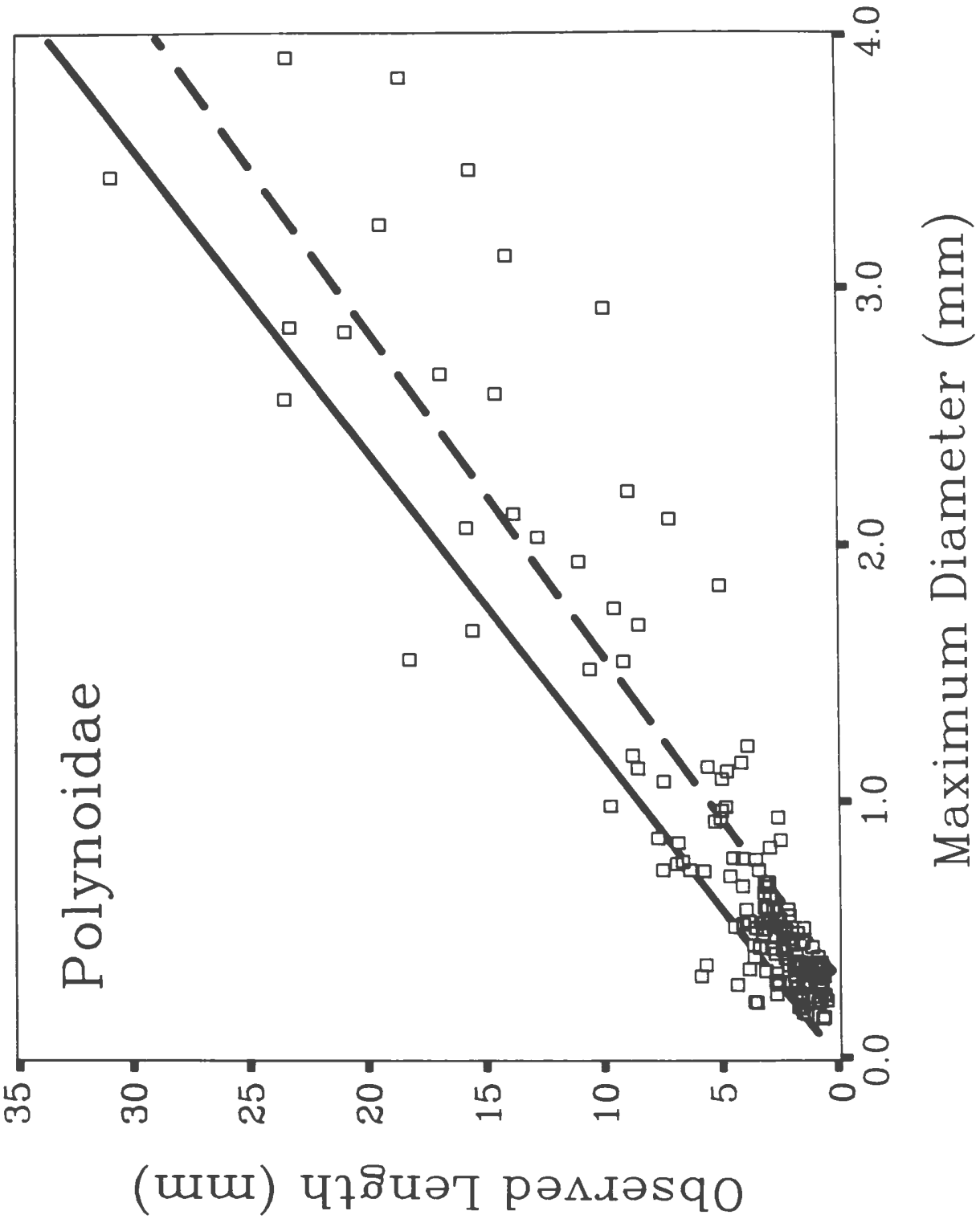

Oweniidae
(Myriochele sp.)
Observed Length (mm)
Maximum Diameter (mm)
0
10
20
30
40
.2
.4
.6
.8
1.0
1.2
1.4
1.6
1.8

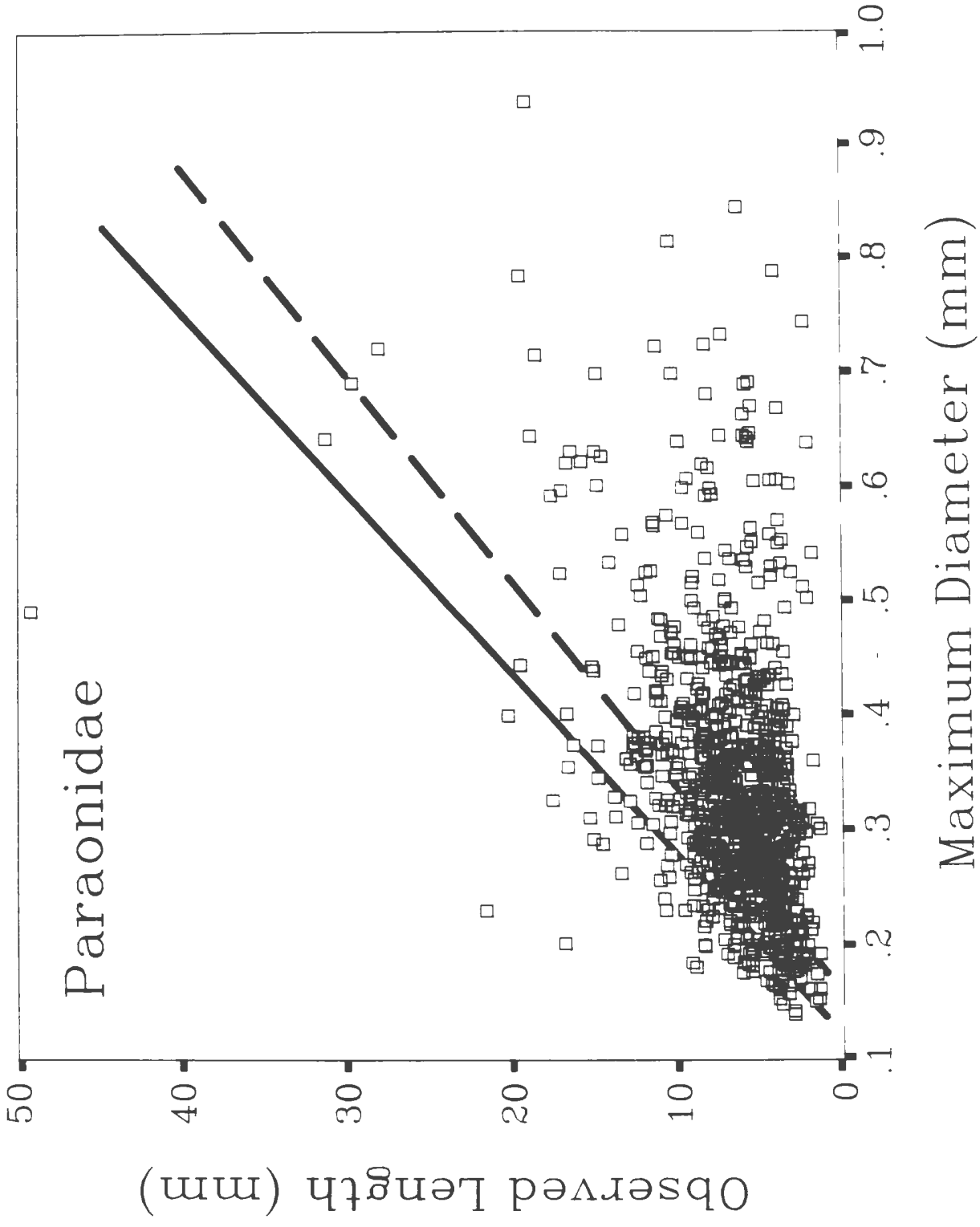

Oweniidae (part)
(Myriochele sp.)
Observed Length (mm)
Maximum Diameter (mm)
0
10
20
30
40
.2
.4
.6

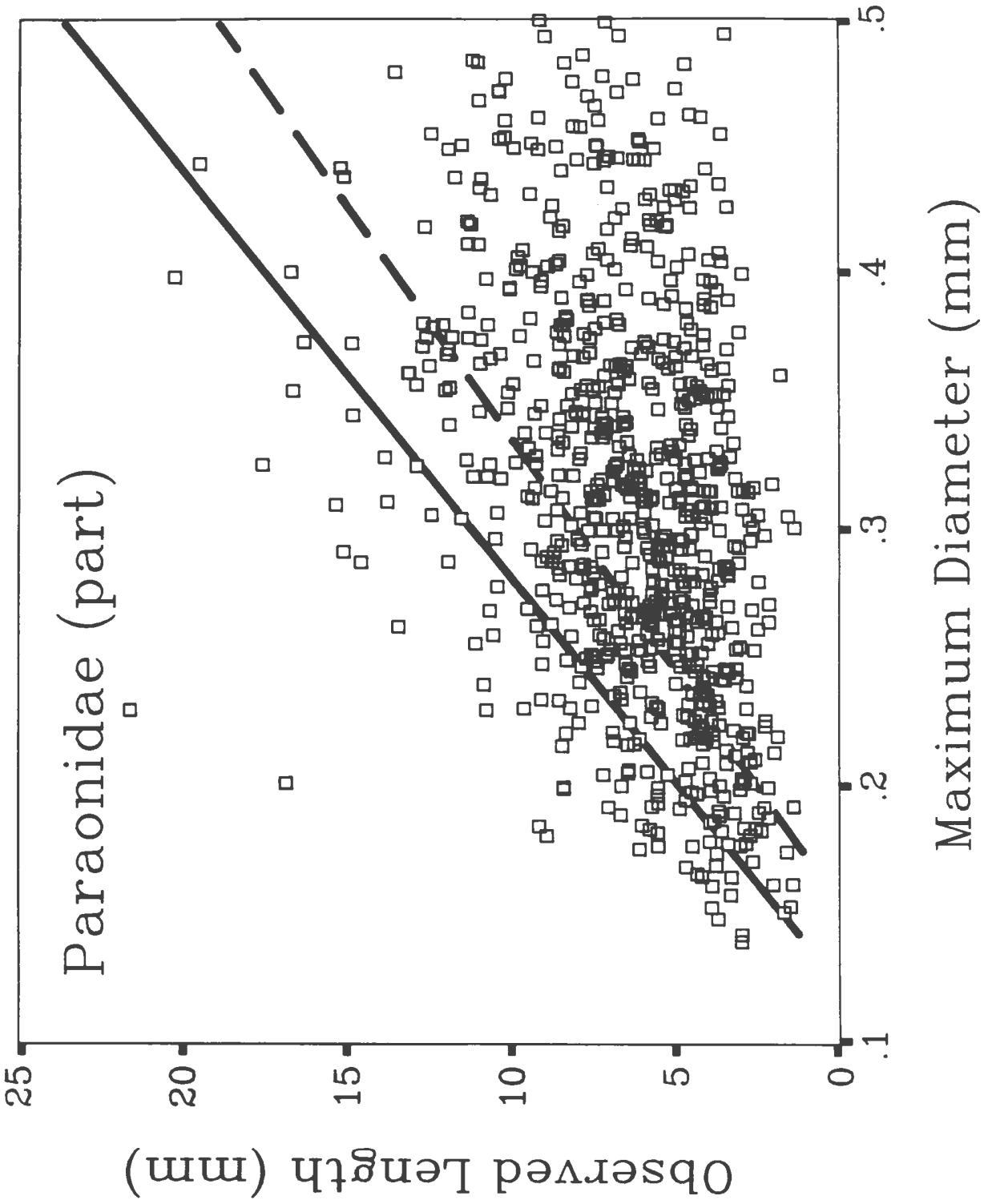

Pectinidae
Observed Length (mm)
Maximum Diameter (mm)
0
10
20
30
40
0
1
2
3
4
5
6

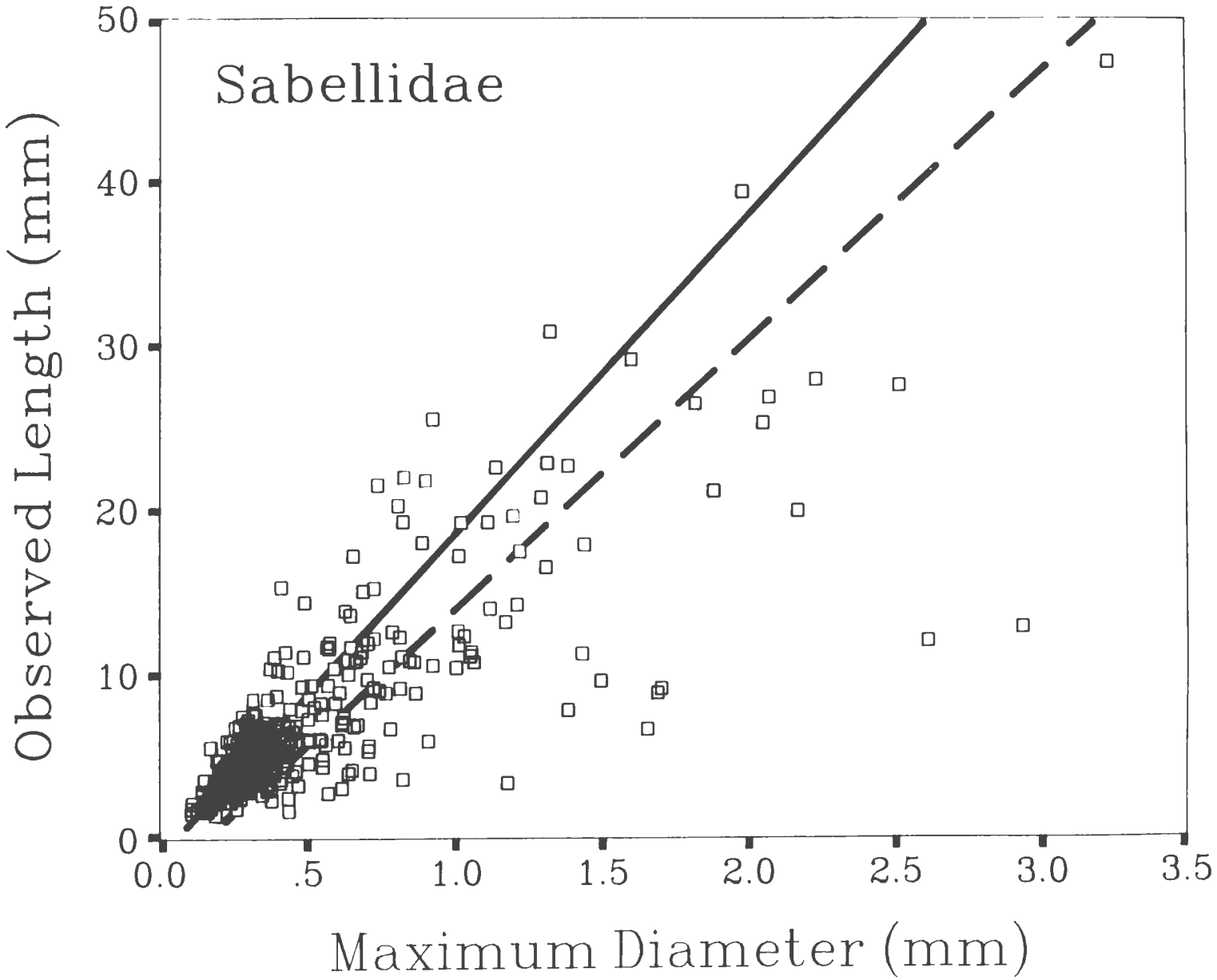

Phyllodocidae
Observed Length (mm)
Maximum Diameter (mm)
0
10
20
30
40
50
60
0.0
.2
.4
.6
.8
1.0
1.2
1.4
1.6
1.8

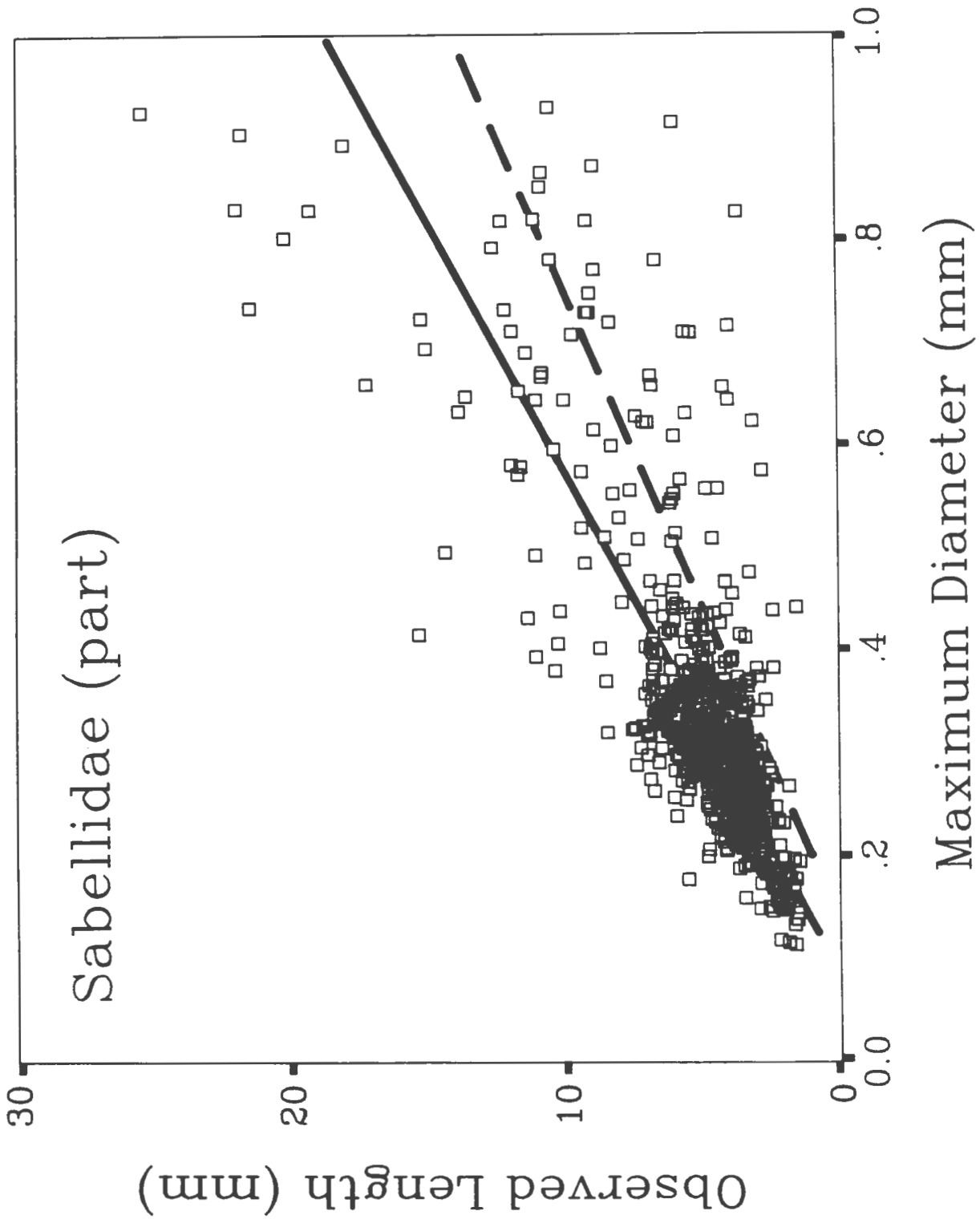

Pilargiidae
Observed Length (mm)
Maximum Diameter (mm)
15
14
13
12
11
10
9
8
7
6
5
4
.2
.4
.6
.8
1.0
1.2
1.4
1.6

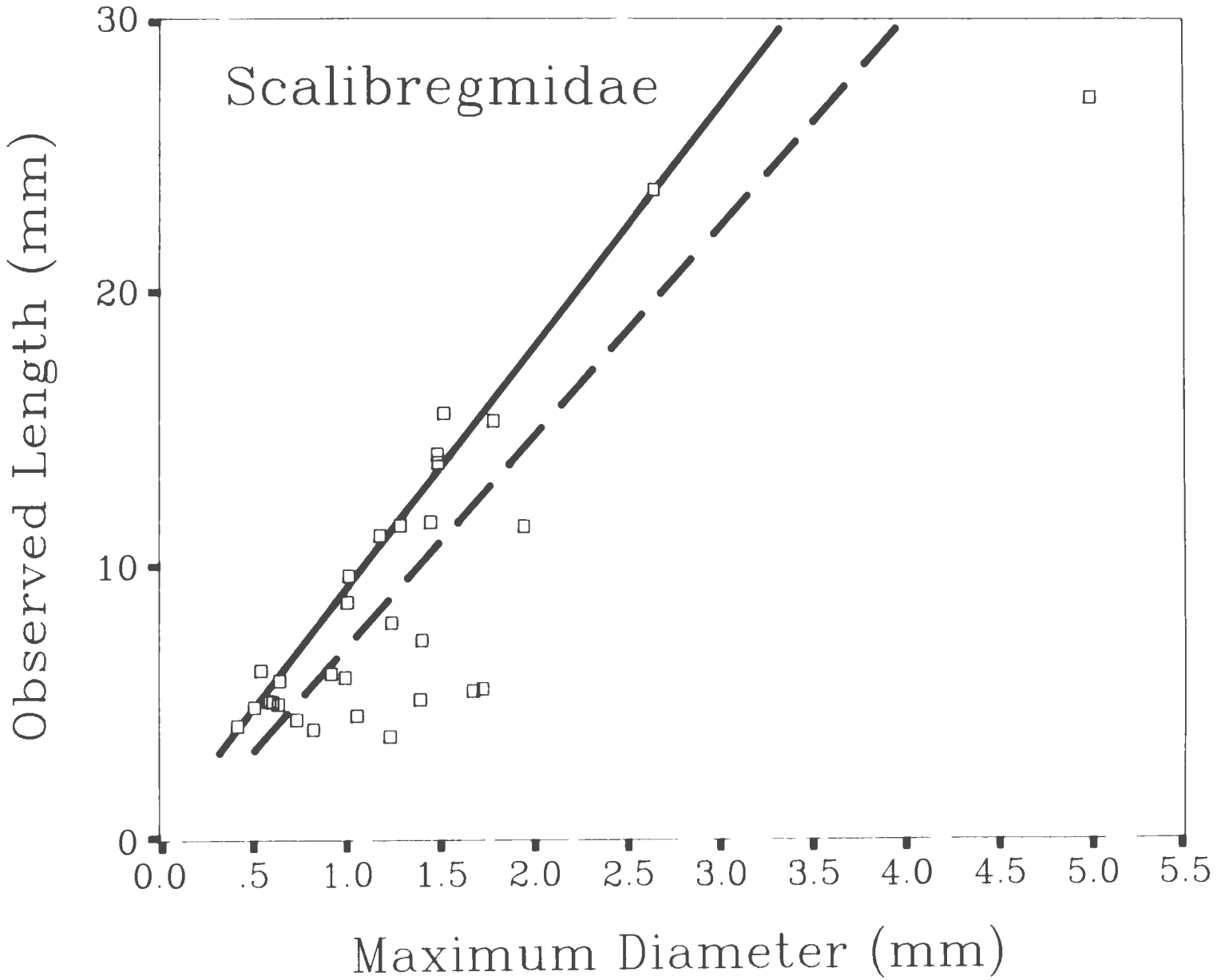

Polynoidae
Observed Length (mm)
Maximum Diameter (mm)
0
5
10
15
20
25
30
35
0.0
1.0
2.0
3.0
4.0

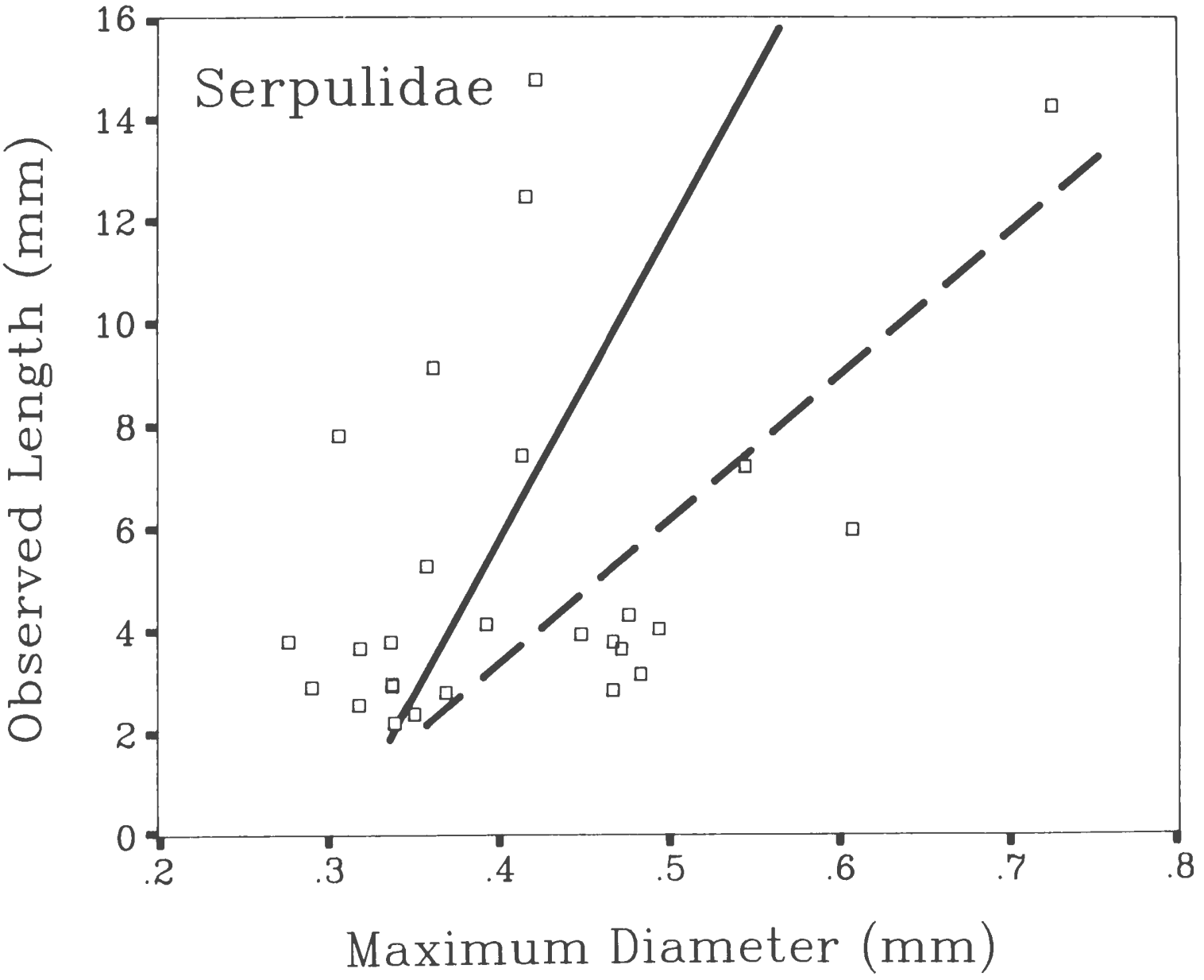

Paraonidae
Observed Length (mm)
Maximum Diameter (mm)
0
10
20
30
40
50
.1
.2
.3
.4
.5
.6
.7
.8
.9
1.0

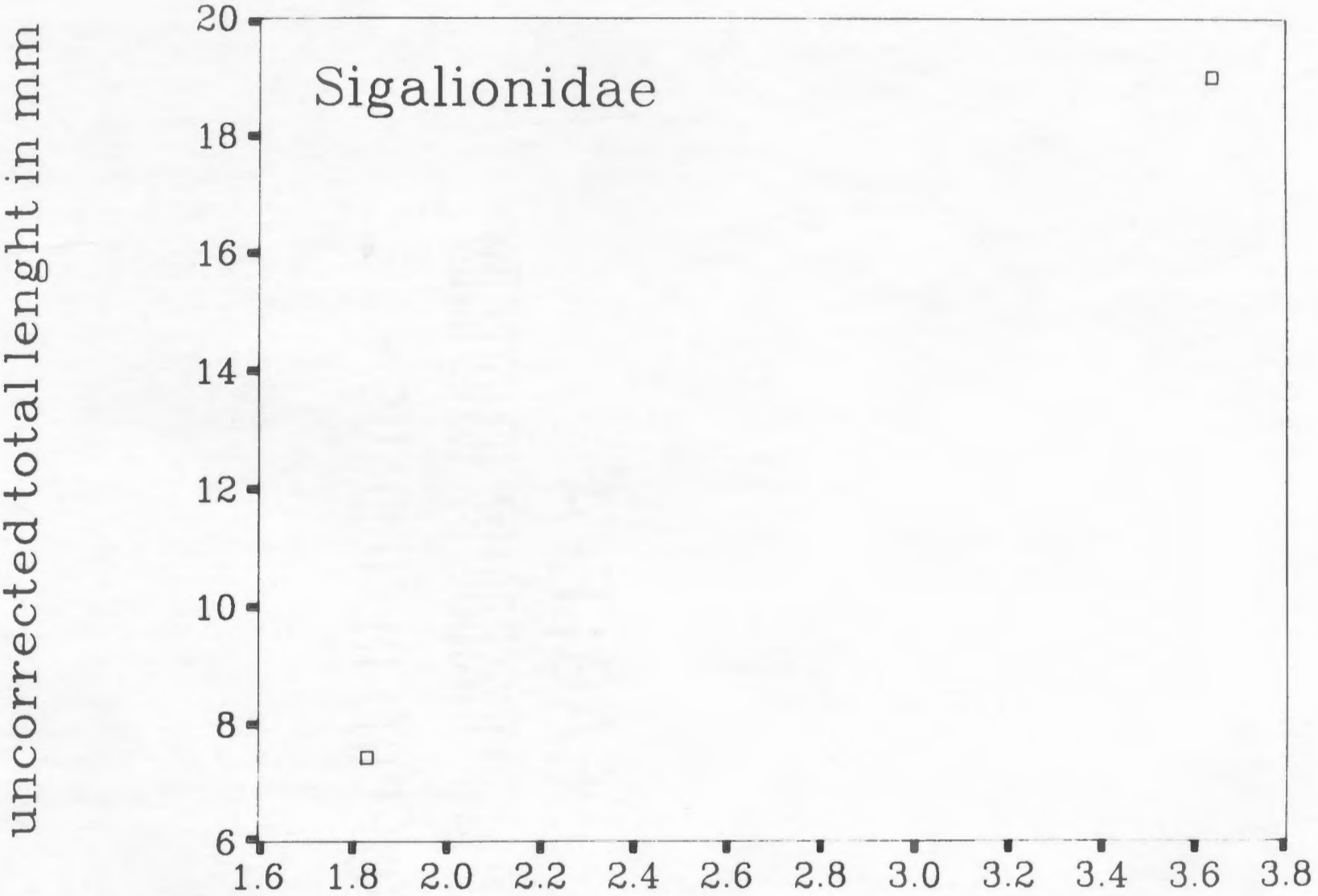

Paraonidae (part)
Observed Length (mm)
Maximum Diameter (mm)
0
5
10
15
20
25
.1
.2
.3
.4
.5

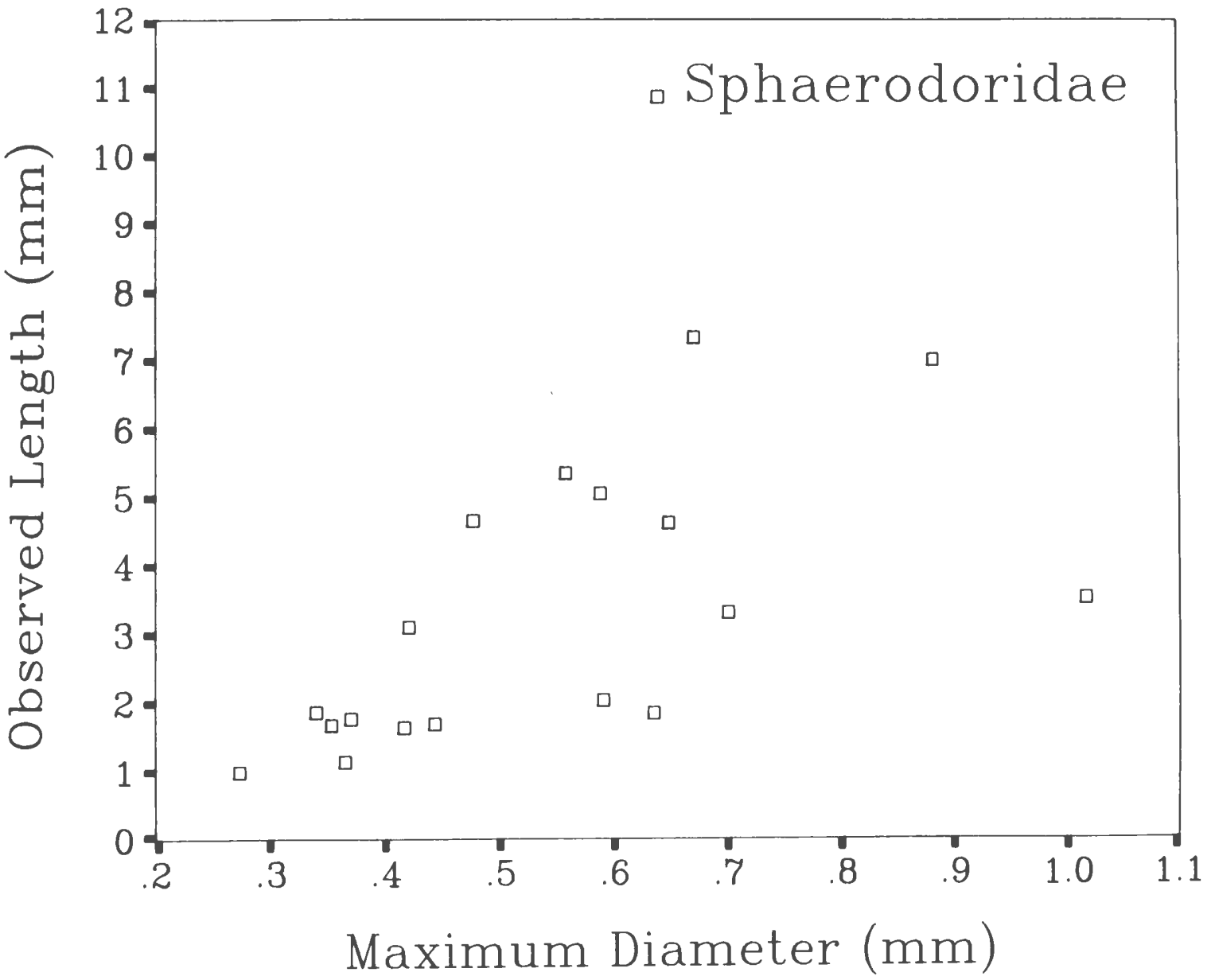

Sabellidae
Observed Length (mm)
Maximum Diameter (mm)
0
10
20
30
40
50
0.0
.5
1.0
1.5
2.0
2.5
3.0
3.5

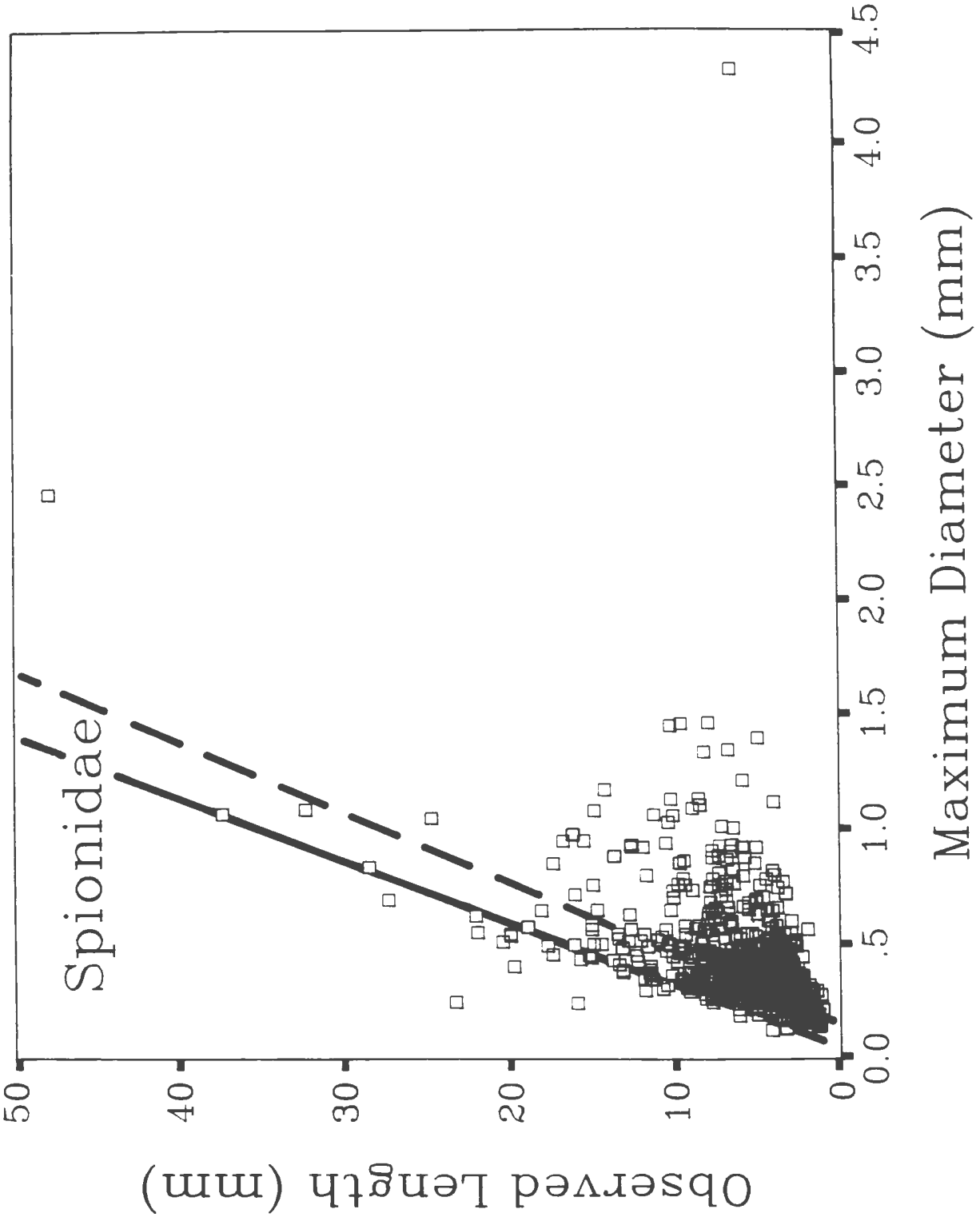

Sabellidae (part)
Observed Length (mm)
Maximum Diameter (mm)
0
10
20
30
0.0
.2
.4
.6
.8
1.0

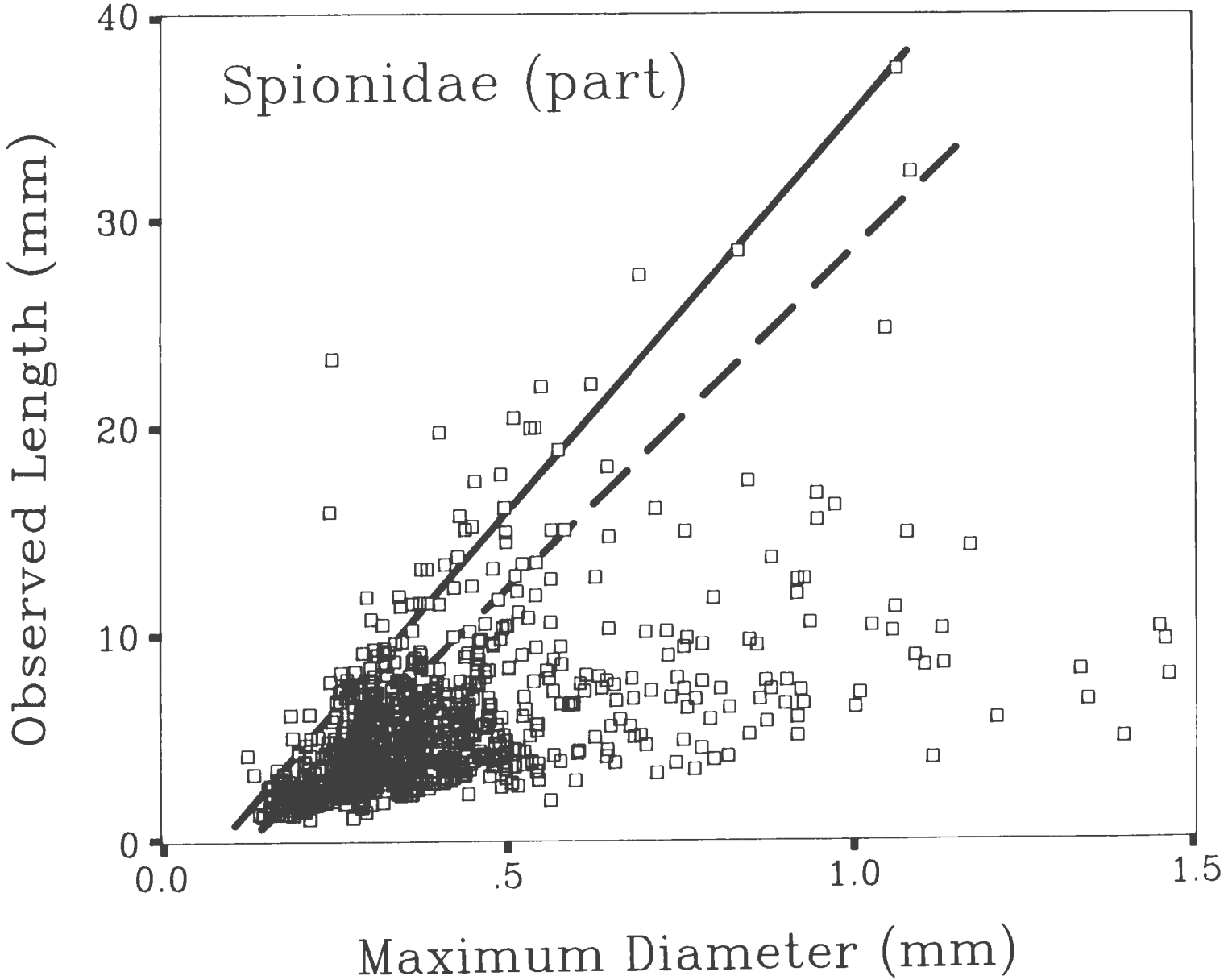

Scalibregmidae
Observed Length (mm)
30
20
10
0
0.0
.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0
4.5
5.0
5.5
Maximum Diameter (mm)

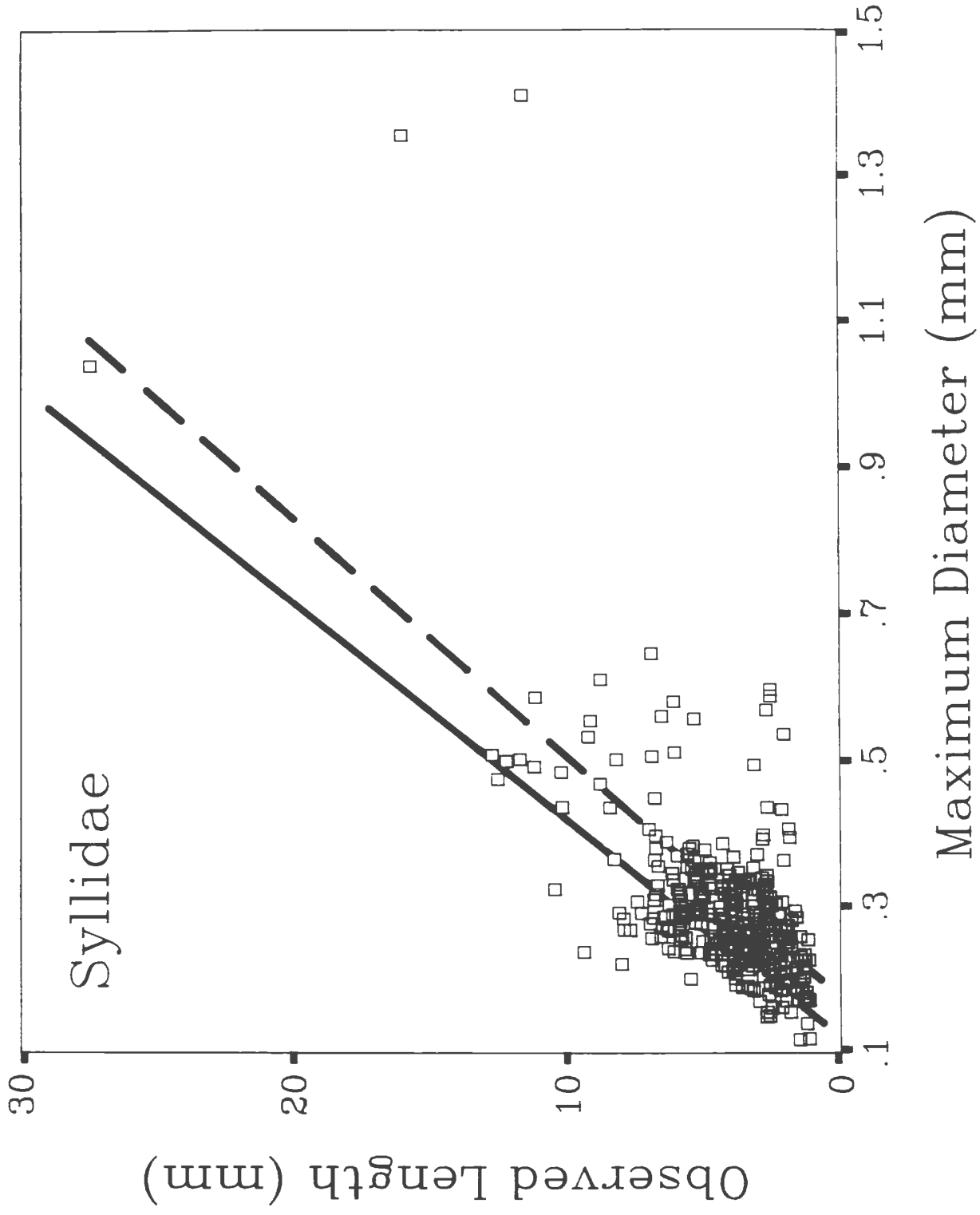

Serpulidae
Observed Length (mm)
Maximum Diameter (mm)
0
2
4
6
8
10
12
14
16
.2
.3
.4
.5
.6
.7
.8

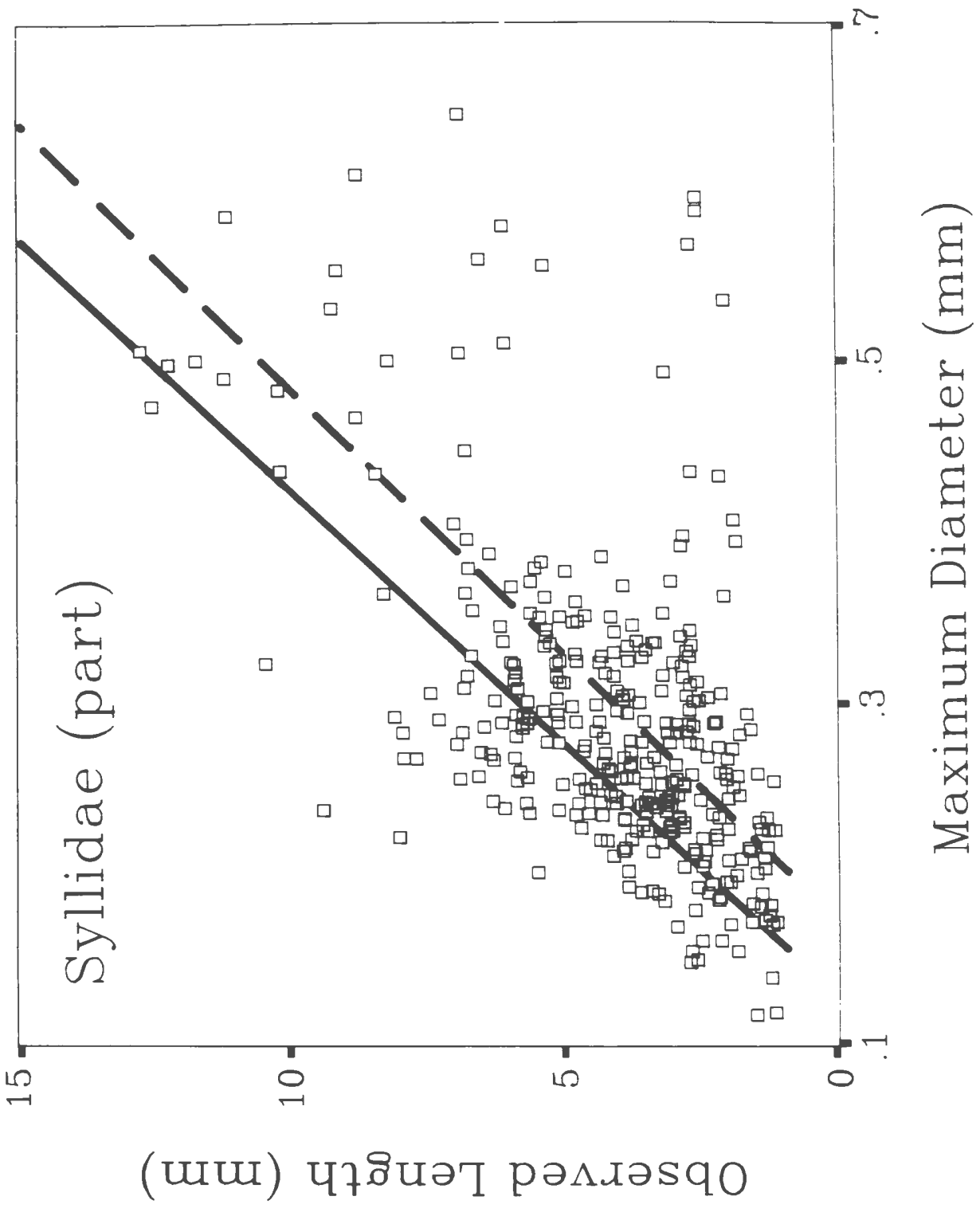

Sigalionidae
uncorrected total lenght in mm
maximum diameter in mm
20
18
16
14
12
10
8
6
1.6
1.8
2.0
2.2
2.4
2.6
2.8
3.0
3.2
3.4
3.6
3.8

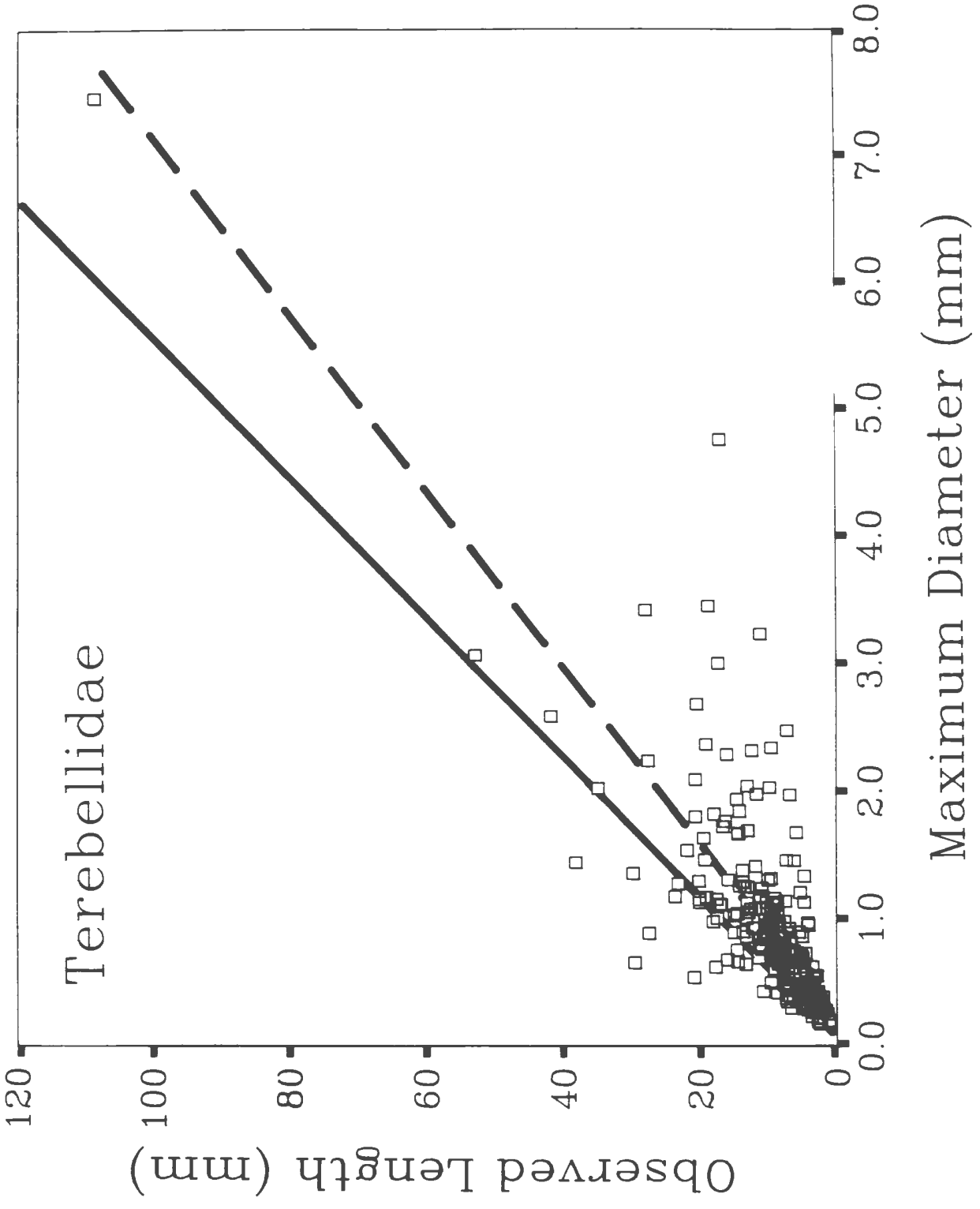

Sphaerodoridae
Observed Length (mm)
Maximum Diameter (mm)
0
1
2
3
4
5
6
7
8
9
10
11
12
.2
.3
.4
.5
.6
.7
.8
.9
1.0
1.1

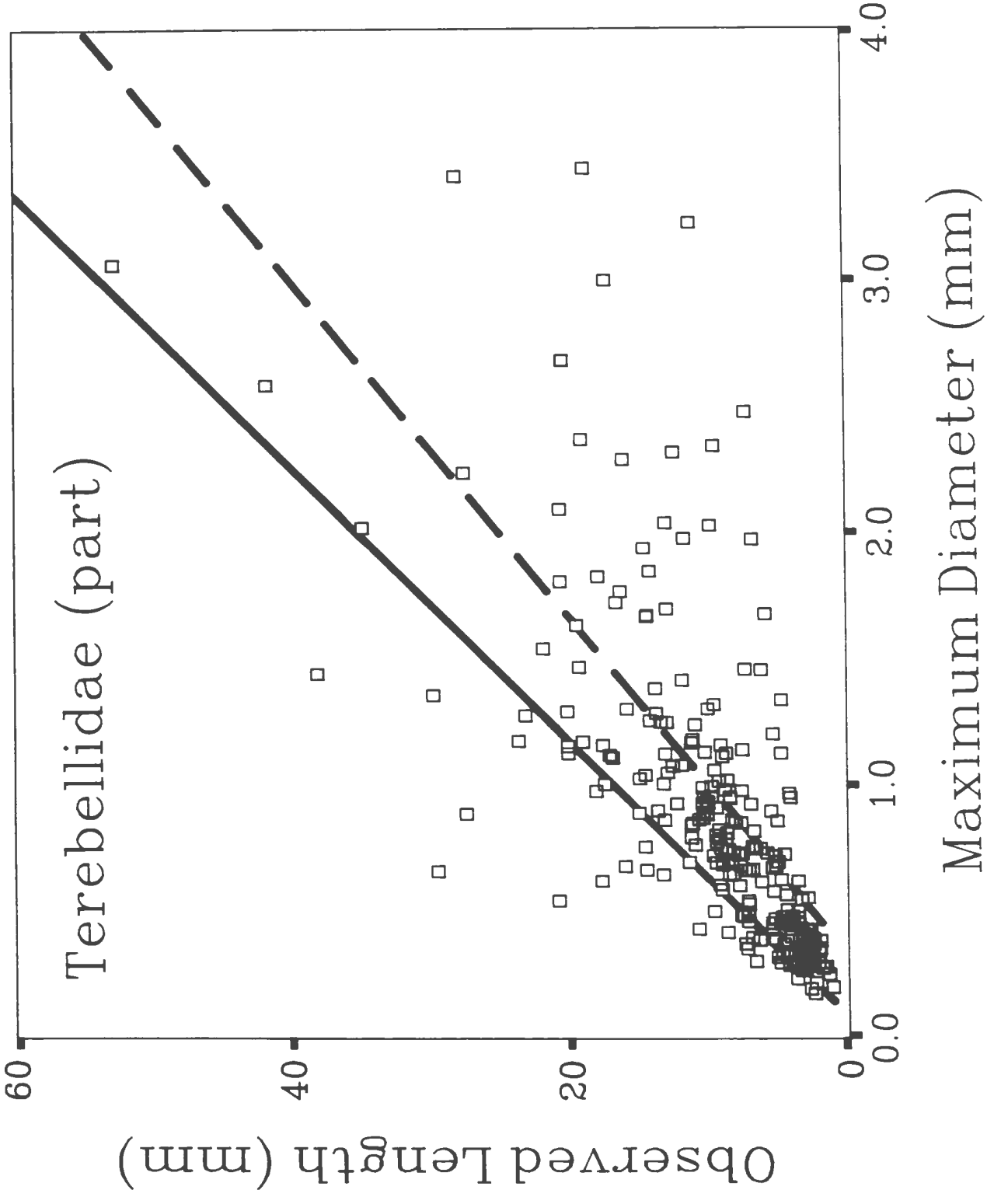

Spionidae
Observed Length (mm)
Maximum Diameter (mm)
0
10
20
30
40
50
0.0
.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0
4.5

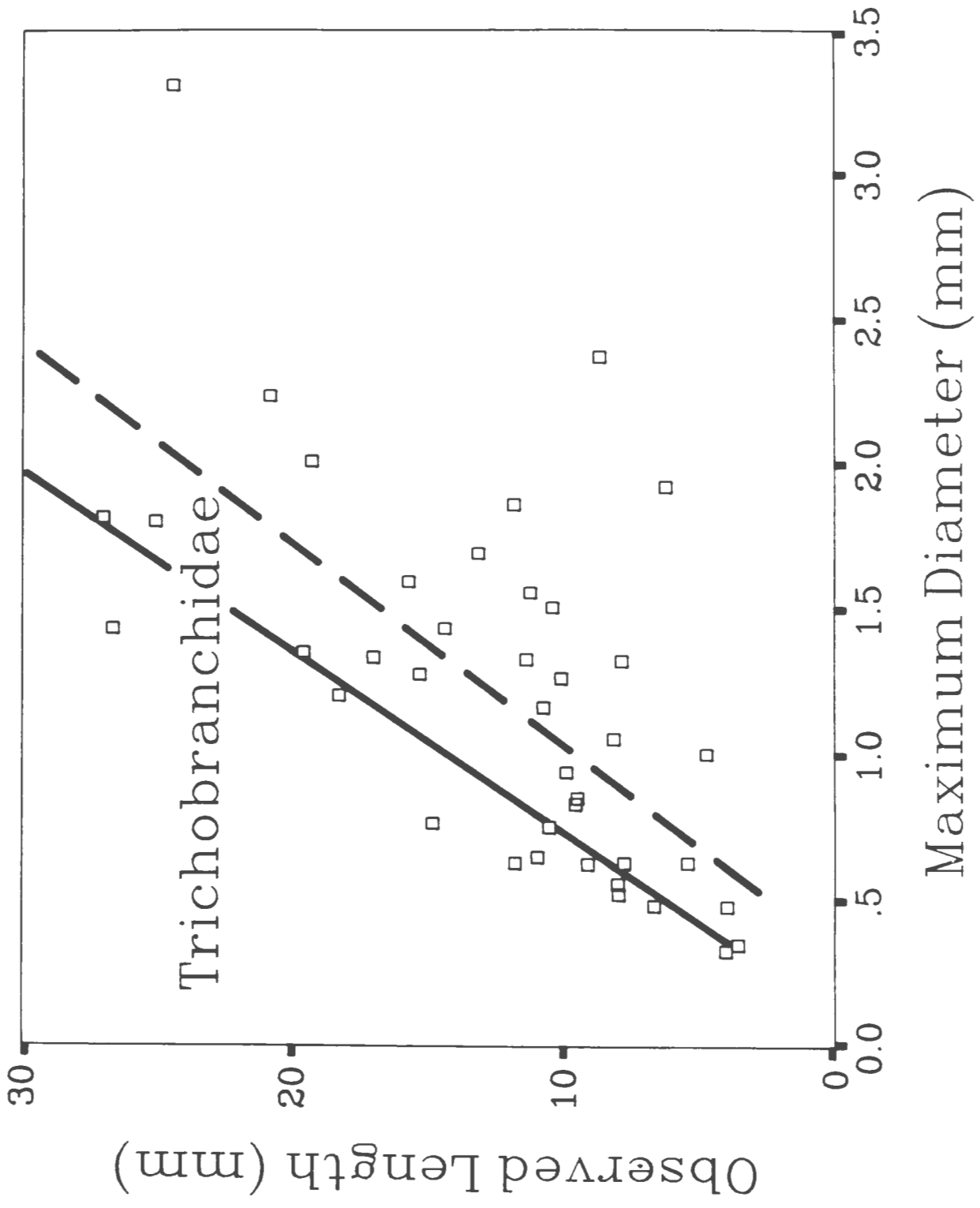

Spionidae (part)
Observed Length (mm)
40
30
20
10
0
0.0
.5
1.0
1.5
Maximum Diameter (mm)

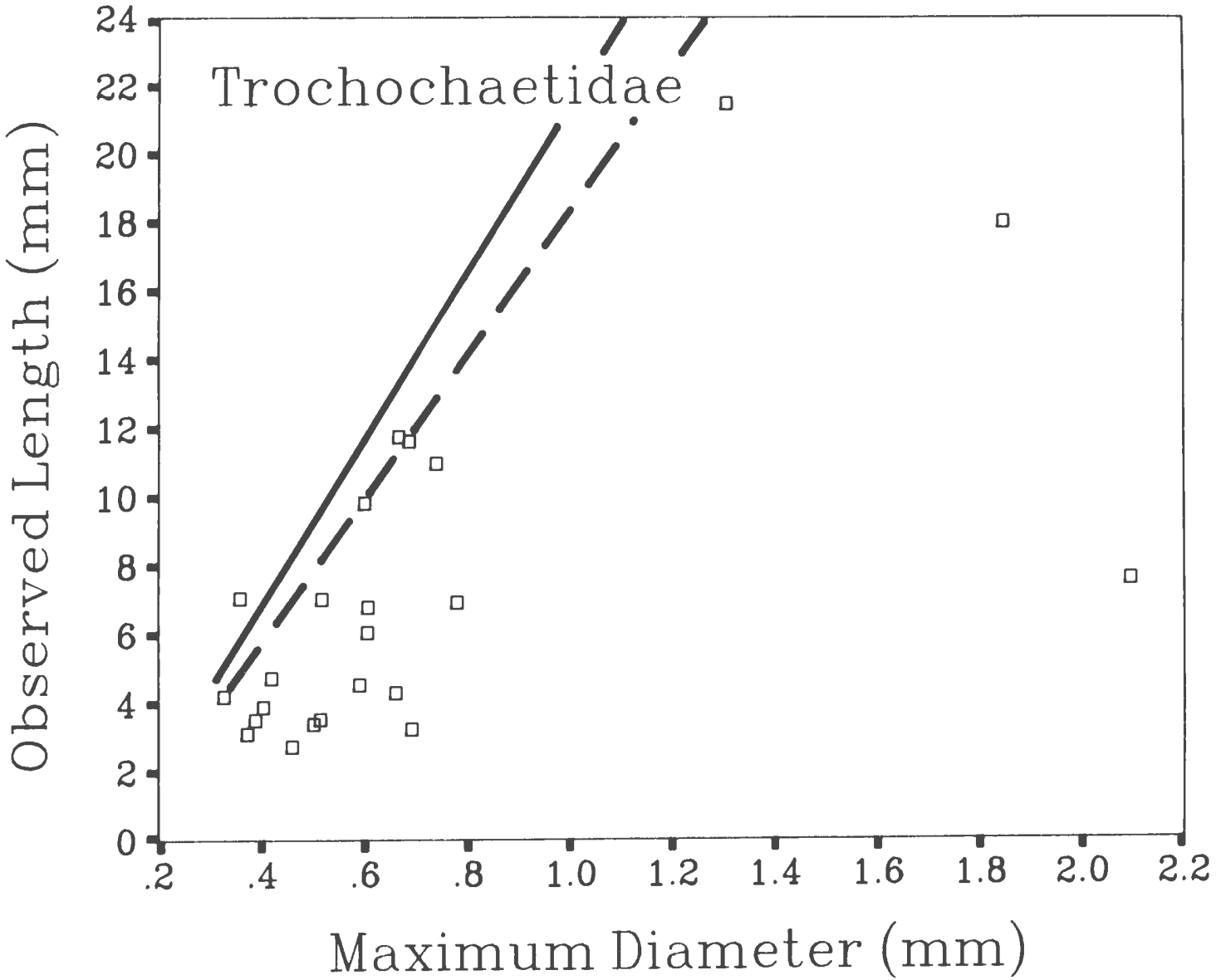

Syllidae
Observed Length (mm)
Maximum Diameter (mm)
0
10
20
30
.1
.3
.5
.7
.9
1.1
1.3
1.5


Syllidae (part)
Observed Length (mm)
Maximum Diameter (mm)
15
10
5
0
.1
.3
.5
.7


Terebellidae
Observed Length (mm)
Maximum Diameter (mm)
0
20
40
60
80
100
120
0.0
1.0
2.0
3.0
4.0
5.0
6.0
7.0
8.0


Terebellidae (part)
Observed Length (mm)
Maximum Diameter (mm)
0
20
40
60
0.0
1.0
2.0
3.0
4.0


Trichobranchidae
Observed Length (mm)
Maximum Diameter (mm)
0
10
20
30
0.0
.5
1.0
1.5
2.0
2.5
3.0
3.5


Trochochaetidae
Observed Length (mm)
Maximum Diameter (mm)
0
2
4
6
8
10
12
14
16
18
20
22
24
.2
.4
.6
.8
1.0
1.2
1.4
1.6
1.8
2.0
2.2

Appendix C

Environmental data

Table C-1. Environmental variable labels used in the multivariate analyses and in Table C-2.

NEWLAT:	Station latitude
DEPTH:	Water depth (m)
SHORE:	Distance from shore (km)
200M:	Distance from 200 m isobath (km)
2000M:	Distance from 2000 m isobath (km)
POLYWT:	Polychaete biomass
TOTALWT:	Total macrofaunal biomass
SILT:	% silt in sediment
CLAY:	% clay in sediment
SAND:	% sand in sediment
GRAVEL:	% gravel in sediment
CURRENT:	Water current regime
PREDTEMP:	Average water temperature (°C)
TEMPRANG:	Average range in water temperature (°C)
PREDSALI:	Average salinity (‰)
SALIRANG:	Average range in salinity (‰)

Table C-2. Environmental data from each sampling site on the Labrador continental shelf and slope and Hermitage Channel.

STATION	NEWLAT	DEPTH	SHORE	200M	2000M
1	2156.4	594	173.2	123.4	131.4
3	2113.9	618	94.8	75.8	180.2
4	2090.0	385	45.3	27.7	212.8
5	2058.6	438	162.8	59.2	58.3
6	2038.8	318	119.9	17.9	88.1
8	2001.7	128	23.1	23.7	177.6
10	1974.7	183	121.4	14.2	85.8
11	1951.2	146	82.5	51.6	144.5
12	1936.4	128	52.0	77.3	168.4
15	1894.0	155	72.5	12.2	126.4
17	1910.3	144	72.5	28.9	117.1
19	1861.2	164	96.4	7.9	121.2
22	1783.2	165	18.9	6.5	139.5
23	1796.1	237	55.9	4.3	94.2
24	1801.8	146	71.2	-7.0	87.9
28	1713.9	157	109.9	3.1	64.6
30	1689.0	136	29.6	5.6	138.8
36	1607.3	420	88.8	23.1	109.2
38	1577.3	622	123.9	25.9	19.4
39	1555.0	135	68.4	-20.7	75.8
40	1545.8	85	54.6	-14.4	90.7
41	1533.3	560	21.3	3.7	119.0
78	1478.7	109	23.5	8.5	125.8
79	1488.3	164	52.3	2.8	92.5
80	1504.1	255	106.4	34.7	48.6
84	1431.4	178	125.8	-2.8	116.7
85	1421.3	152	88.3	15.2	171.5
87	1413.1	219	60.5	12.6	207.4
88	1309.8	140	17.6	35.2	231.3
89	1325.6	285	56.2	4.6	187.6
90	1343.4	166	93.8	8.9	145.4
91	1362.5	201	152.1	1.9	88.6
94	1271.5	225	199.2	6.8	85.5
1526	748.3	375	13.3	11.1	388.5
1528	748.4	330	13.3	11.1	388.5
1529	748.5	305	13.3	11.1	388.5

Table C-2. Continued.

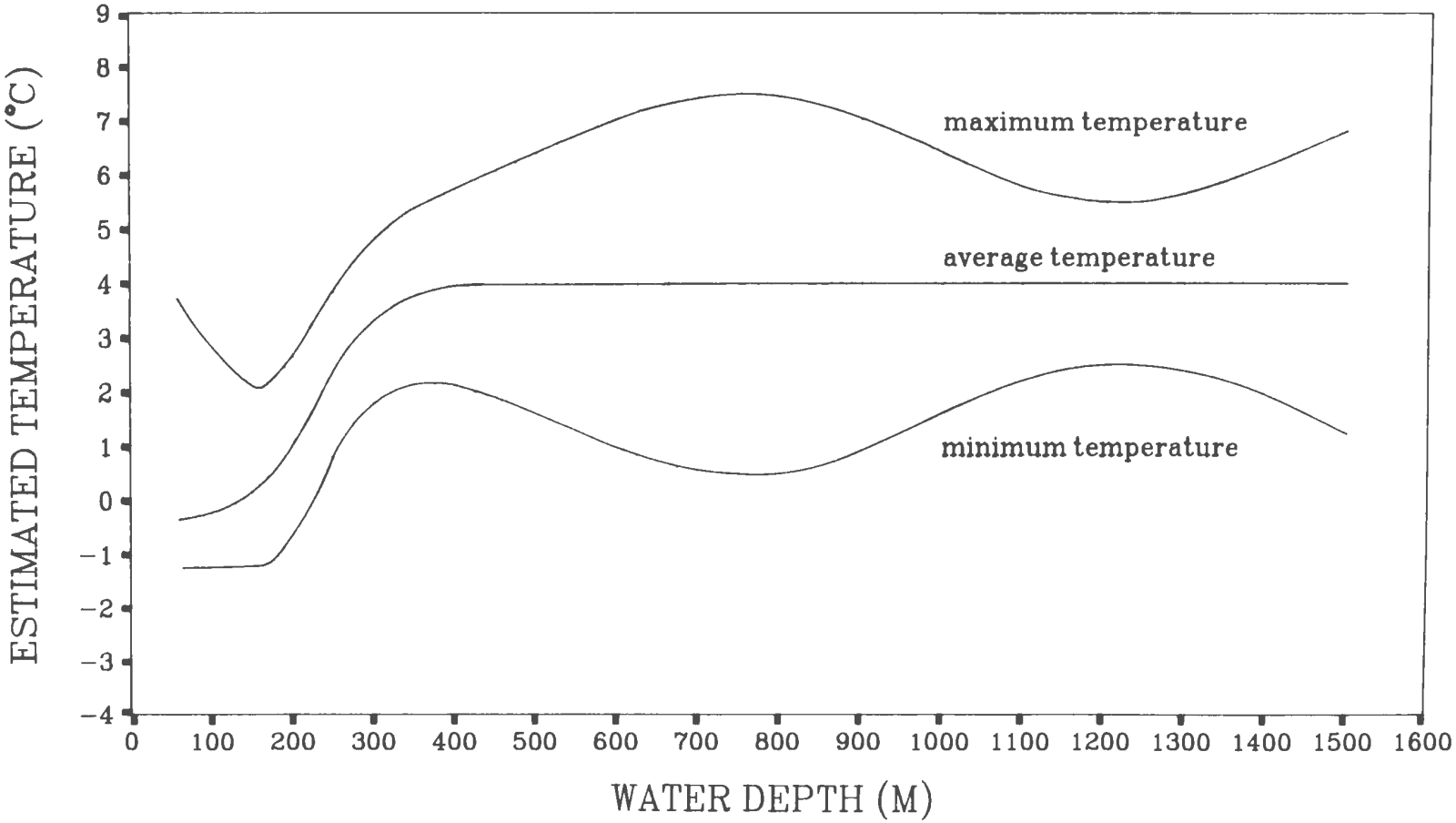
STATION	POLYWT	TOTALWT	SILT	CLAY	SAND	GRAVEL
1	0.06	0.06	44.3	28.2	21.7	5.8
3	0.50	0.80	7.1	11.7	63.1	18.2
4	6.73	6.77	11.3	12.7	34.3	41.7
5	6.05	7.16	39.2	36.3	21.1	3.3
6	0.84	6.12	33.3	30.6	29.3	6.7
8	44.23	1261.90	30.7	20.8	32.7	15.9
10	50.08	919.62	8.6	13.0	72.8	5.5
11	15.05	559.80	7.4	17.2	73.4	1.9
12	165.47	338.65	14.1	28.1	49.5	8.2
15	49.64	403.58	9.1	51.9	36.9	2.1
17	57.62	695.29	6.2	26.9	54.4	12.5
19	297.17	448.41	23.3	38.8	37.4	0.5
22	27.51	783.66	8.8	9.5	80.4	1.3
23	15.31	500.99	17.5	32.0	46.4	4.2
24	49.94	1077.31	8.5	13.2	39.4	38.9
28	305.42	2274.11	4.3	4.4	91.1	0.2
30	57.95	772.69	8.0	7.4	66.0	18.6
36	17.31	19.31	41.2	44.1	14.7	0.0
38	150.49	177.62	13.1	11.6	72.2	3.1
39	109.44	1008.30	3.0	2.5	88.7	5.8
40	50.93	102.29	2.7	3.3	45.1	48.9
41	73.86	112.25	59.7	36.4	3.9	0.0
78	8.57	389.75	1.2	1.0	39.5	58.3
79	56.75	350.51	14.4	16.8	46.0	22.8
80	29.76	542.59	5.2	3.9	81.4	9.4
84	6.56	27.74	4.0	9.2	86.6	0.1
85	18.99	159.31	2.7	3.6	93.7	0.0
87	56.08	90.75	6.1	5.4	73.3	15.2
88	15.70	535.74	22.7	24.3	46.3	6.7
89	48.06	178.78	5.3	6.2	50.9	37.7
90	2.75	2.83	1.8	8.5	89.7	0.0
91	25.56	63.50	4.3	9.8	86.0	0.0
94	19.28	55.09	4.9	12.8	82.4	0.0
1526	2.68	4.00	47.4	49.0	3.7	0.0
1528	25.32	250.00	22.5	30.4	38.6	8.5
1529	15.54	150.00	25.2	36.1	34.4	4.2

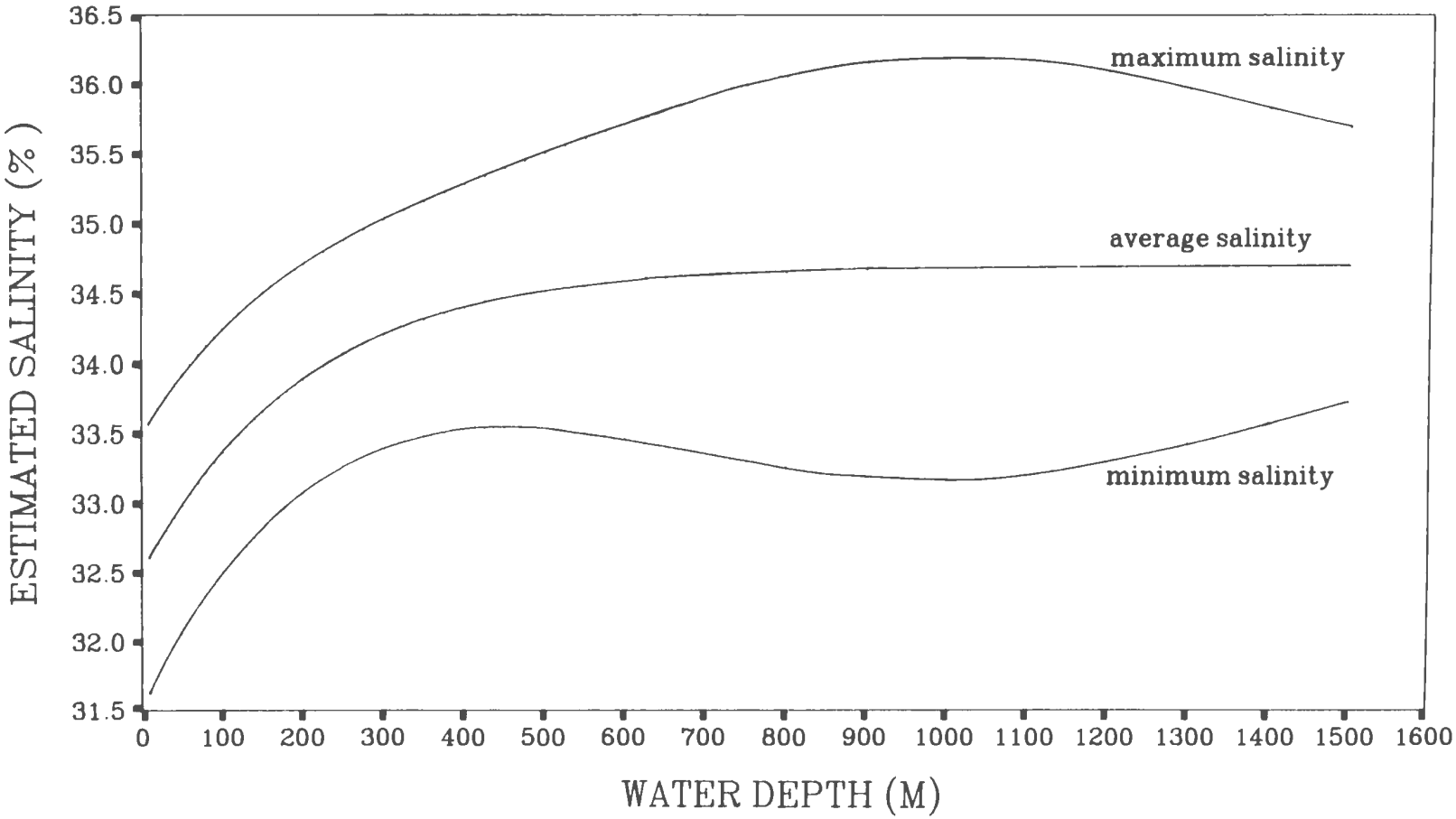
Table C-2. Continued.

STATION	CURRENT	PREDTEMP	TEMPRANG	PREDSALI	SALIRANG
1	3.0	4.93	6.03	34.59	2.24
3	4.0	4.85	6.29	34.60	2.31
4	4.0	4.71	3.51	34.38	1.74
5	4.0	4.73	4.05	34.45	1.84
6	3.5	4.25	3.08	34.25	1.66
8	3.0	0.57	3.87	33.54	1.72
10	1.5	1.27	3.36	33.82	1.66
11	1.0	0.65	3.68	33.64	1.70
12	1.0	0.46	3.87	33.54	1.72
15	1.0	0.66	3.60	33.69	1.68
17	1.0	0.56	3.70	33.63	1.70
19	1.0	0.73	3.52	33.73	1.67
22	2.5	0.60	3.51	33.74	1.67
23	2.0	2.27	3.06	34.03	1.63
24	2.0	0.38	3.68	33.64	1.70
28	1.0	0.36	3.58	33.70	1.68
30	3.0	0.08	3.79	33.59	1.71
36	3.0	3.90	3.85	34.43	1.80
38	4.0	3.89	6.33	34.60	2.32
39	1.0	-0.17	3.80	33.58	1.71
40	1.0	-0.47	4.38	33.26	1.79
41	3.0	3.81	5.62	34.57	2.14
78	3.0	-0.49	4.09	33.42	1.75
79	1.5	0.06	3.52	33.73	1.67
80	2.0	2.20	3.02	34.09	1.63
84	1.0	0.19	3.40	33.80	1.66
85	1.0	-0.23	3.63	33.67	1.69
87	3.0	1.10	3.14	33.96	1.64
88	2.5	-0.57	3.75	33.61	1.70
89	3.0	2.51	3.00	34.17	1.64
90	1.5	-0.17	3.50	33.74	1.67
91	1.5	0.56	3.23	33.90	1.64
94	3.5	1.01	3.11	33.99	1.63
1526	3.5	5.00	2.00	34.50	0.60
1528	3.5	5.00	2.00	34.50	0.60
1529	3.5	5.00	2.00	34.50	0.60

Appendix D

Fitted temperature and salinity curves from data in Lazier (1982)


ESTIMATED TEMPERATURE (°C)
9
8
7
6
5
4
3
2
1
0
−1
−2
−3
−4
maximum temperature
average temperature
minimum temperature
0
100
200
300
400
500
600
700
800
900
1000
1100
1200
1300
1400
1500
1600
WATER DEPTH (M)


ESTIMATED SALINITY (%)
36.5
36.0
35.5
35.0
34.5
34.0
33.5
33.0
32.5
32.0
31.5
maximum salinity
average salinity
minimum salinity
0
100
200
300
400
500
600
700
800
900
1000
1100
1200
1300
1400
1500
1600
WATER DEPTH (M)

Appendix E

Frequencies of polychaetes for the functional and taxonomic approaches

Table E-1. Absolute frequencies of benthic polychaetes per station in each attribute of functional approaches based on **feeding type**, **feeding microhabitat** and **motility pattern**. See text for detailed descriptions of attributes. Attribute codes are defined in Figure 2.

		FEEDING		MICROHABITAT				MOTILITY			
STATION	DEPTH	MA	MI	WA	SR	SB	WS	MO	DM	SE	SD
1/L-1	594	3	11	0	11	3	0	6	6	2	0
3/L-2	618	2	3	0	5	0	0	0	3	2	0
4/L-3	385	3	21	0	6	18	0	5	0	19	0
5/L-4	438	7	25	3	29	0	0	4	8	20	0
6/L-5	318	1	19	15	4	1	0	1	1	18	0
8/L-7	128	41	151	45	83	30	34	47	76	45	24
10/L-9	183	25	211	7	125	59	45	91	53	50	42
11/L-10	183	44	150	31	90	10	63	85	44	2	63
12/L-11	128	9	74	13	57	11	2	36	34	11	2
15/L-13	155	230	332	168	264	25	105	259	194	18	91
17/L-14	144	87	112	20	135	6	38	108	46	7	38
19/L-15	164	317	80	3	352	19	23	336	28	10	23
22/L-16	165	33	112	15	91	24	15	95	33	2	15
23/L-17	237	10	98	4	55	40	9	40	21	38	9
24/L-18	146	69	281	30	172	133	15	115	85	140	10
28/L-19	157	206	89	3	257	30	5	238	45	11	1
30/L-20	136	23	53	2	52	20	2	49	18	7	2
36/L-22	420	23	94	2	83	32	0	77	19	21	0
38/L-23	622	9	19	9	13	5	1	9	11	7	1
39/L-24	135	82	93	3	132	40	0	116	15	44	0
40/L-25	85	15	32	7	23	12	5	16	5	22	4
41/L-26	560	5	30	0	25	8	2	12	8	13	2
78/L-27	109	33	84	19	71	13	14	48	31	24	14
79/L-28	164	121	211	20	219	79	14	149	60	110	13
80/L-29	255	36	302	41	161	110	26	151	63	102	22
84/L-31	220	49	119	7	106	20	35	81	42	10	35
85/L-32	152	46	182	32	130	25	41	72	93	23	40
87/L-33	219	215	229	19	370	36	19	308	77	40	19
88/L-34	140	278	669	115	542	112	178	476	266	27	178
89/L-35	285	61	238	18	177	58	46	128	64	66	41
90/L-36	166	25	40	0	46	2	17	36	10	2	17
91/L-37	201	66	164	2	114	61	53	108	31	47	44
94/L-38	225	13	191	18	61	111	14	65	47	85	7
HC_1526	375	25	13	1	33	4	0	25	8	5	0
HC_1528	330	165	461	25	524	67	10	270	271	75	10
HC_1529	305	105	253	8	305	42	3	175	160	20	3

Table E-2. Absolute frequencies of benthic polychaetes per station in each size class of the functional design based on **body size** See text for detailed descriptions of size classes.

		SIZE CLASSES					
STATION	DEPTH	1	2	3	4	5	6
1/L-1	594	0	0	12	1	1	0
3/L-2	618	0	1	1	2	1	0
4/L-3	385	0	2	7	14	1	0
5/L-4	438	0	2	15	14	0	1
6/L-5	318	0	0	10	5	5	0
8/L-7	128	2	61	67	39	22	1
10/L-9	183	2	47	116	58	9	4
11/L-10	183	0	68	100	20	4	2
12/L-11	128	0	26	38	11	4	4
15/L-13	155	13	298	206	25	14	6
17/L-14	144	0	59	105	22	9	4
19/L-15	164	0	73	113	30	171	10
22/L-16	165	2	58	56	18	9	2
23/L-17	237	0	14	45	40	7	2
24/L-18	146	2	50	143	139	13	3
28/L-19	157	5	46	46	43	151	4
30/L-20	136	0	19	30	20	7	0
36/L-22	420	7	51	24	24	11	0
38/L-23	622	0	1	7	9	9	2
39/L-24	135	3	23	62	28	53	6
40/L-25	85	0	12	18	16	0	1
41/L-26	560	0	3	16	4	12	0
78/L-27	109	2	45	39	25	4	2
79/L-28	164	1	82	108	69	65	7
80/L-29	255	1	53	196	76	10	2
84/L-31	220	2	60	76	22	7	1
85/L-32	152	5	96	70	52	5	0
87/L-33	219	2	125	127	67	121	2
88/L-34	140	251	512	157	20	5	2
89/L-35	285	1	86	113	80	13	6
90/L-36	166	1	26	25	10	2	0
91/L-37	201	2	50	100	58	20	0
94/L-38	225	0	21	105	69	9	0
HC_1526	375	0	6	18	13	1	0
HC_1528	330	38	262	275	37	13	1
HC_1529	305	30	171	126	23	7	1

Table E-3. Absolute frequencies of benthic polychaetes per station in each attribute of the functional approach based on **foraging mode** and **body size**. See text for detailed descriptions of attributes. Attribute codes are defined in Figure 2.

		MASRMO				MASRDM			
STATION	DEPTH	1	2	3	4	1	2	3	4
1/L-1	594	0	3	0	0	0	0	0	0
3/L-2	618	0	0	0	0	0	1	1	0
4/L-3	385	1	0	2	0	0	0	0	0
5/L-4	438	0	2	1	0	0	2	1	1
6/L-5	318	0	0	1	0	0	0	0	0
8/L-7	128	5	17	17	0	0	0	2	0
10/L-9	183	9	9	5	1	0	1	0	0
11/L-10	183	11	29	4	0	0	0	0	0
12/L-11	128	1	5	1	2	0	0	0	0
15/L-13	155	94	132	3	1	0	0	0	0
17/L-14	144	20	54	11	2	0	0	0	0
19/L-15	164	53	80	175	9	0	0	0	0
22/L-16	165	10	20	2	1	0	0	0	0
23/L-17	237	1	6	3	0	0	0	0	0
24/L-18	146	17	31	6	3	1	9	2	0
28/L-19	157	19	17	165	2	1	2	0	0
30/L-20	136	5	13	5	0	0	0	0	0
36/L-22	420	7	9	5	0	0	2	0	0
38/L-23	622	0	1	7	0	0	0	1	0
39/L-24	135	14	5	54	6	0	1	2	0
40/L-25	85	8	5	0	1	1	0	0	0
41/L-26	560	0	2	3	0	0	0	0	0
78/L-27	109	20	6	3	0	1	2	0	1
79/L-28	164	39	10	57	7	0	2	6	0
80/L-29	255	4	15	7	2	2	4	2	0
84/L-31	220	27	22	0	0	0	0	0	0
85/L-32	152	34	5	2	0	1	3	1	0
87/L-33	219	35	35	135	2	0	6	2	0
88/L-34	140	254	18	1	1	1	2	1	0
89/L-35	285	18	31	7	0	2	3	0	0
90/L-36	166	21	3	0	0	0	0	0	0
91/L-37	201	13	20	33	0	0	0	0	0
94/L-38	225	2	4	7	0	0	0	0	0
HC_1526	375	4	19	1	0	0	0	1	0
HC_1528	330	80	72	9	0	2	1	1	0
HC_1529	305	54	48	2	0	1	0	0	0

Table E-3. (Continued)

	MISRMO				MISBMO			
STATION	1	2	3	4	1	2	3	4
1/L-1	0	0	0	0	0	3	0	0
3/L-2	0	0	0	0	0	0	0	0
4/L-3	0	2	0	0	0	0	0	0
5/L-4	0	1	0	0	0	0	0	0
6/L-5	0	0	0	0	0	0	0	0
8/L-7	1	2	0	0	1	2	2	0
10/L-9	12	39	1	0	1	7	5	2
11/L-10	3	28	0	0	5	1	4	0
12/L-11	6	18	0	0	3	0	0	0
15/L-13	1	7	0	0	4	4	10	3
17/L-14	1	16	0	0	1	2	1	0
19/L-15	2	3	1	0	2	7	3	1
22/L-16	18	22	0	0	4	6	11	1
23/L-17	4	20	0	0	3	2	0	1
24/L-18	11	22	0	0	4	19	2	0
28/L-19	6	6	0	0	5	12	5	1
30/L-20	0	4	2	0	6	8	6	0
36/L-22	39	4	0	0	7	5	1	0
38/L-23	1	0	0	0	0	0	0	0
39/L-24	10	25	1	0	0	1	0	0
40/L-25	0	2	0	0	0	0	0	0
41/L-26	1	2	0	0	0	4	0	0
78/L-27	1	16	0	0	0	0	2	0
79/L-28	9	11	0	0	5	8	3	0
80/L-29	23	83	0	0	5	10	2	0
84/L-31	5	13	0	0	2	9	3	0
85/L-32	10	10	0	0	4	6	1	0
87/L-33	63	35	0	0	1	1	1	0
88/L-34	72	27	0	0	81	18	4	0
89/L-35	20	35	0	0	6	8	3	0
90/L-36	6	5	0	0	0	0	0	0
91/L-37	6	20	0	0	5	8	3	0
94/L-38	3	19	1	0	2	24	3	0
HC_1526	0	0	0	0	0	1	0	0
HC_1528	33	13	1	0	12	45	4	1
HC_1529	26	3	0	0	13	26	3	0

Table E-3. (Continued)

STATION	MIWADM				MISRDM			
	1	2	3	4	1	2	3	4
1/L-1	0	0	0	0	0	6	0	0
3/L-2	0	0	0	0	1	0	0	0
4/L-3	0	0	0	0	0	0	0	0
5/L-4	0	3	0	0	0	1	0	0
6/L-5	0	1	0	0	0	0	0	0
8/L-7	42	2	0	0	1	13	6	0
10/L-9	1	5	1	0	12	28	2	0
11/L-10	31	0	0	0	0	12	0	1
12/L-11	11	0	0	0	3	18	2	0
15/L-13	160	8	0	0	3	8	1	0
17/L-14	18	2	0	0	9	17	0	0
19/L-15	1	1	0	0	7	14	5	0
22/L-16	15	0	0	0	5	11	2	0
23/L-17	0	1	1	0	5	12	2	0
24/L-18	6	17	0	0	7	35	3	0
28/L-19	2	0	0	0	15	17	4	0
30/L-20	0	0	0	0	6	11	1	0
36/L-22	0	0	1	0	2	14	0	0
38/L-23	0	8	1	0	0	1	0	0
39/L-24	0	1	0	0	0	9	2	0
40/L-25	0	0	0	0	0	1	2	0
41/L-26	0	0	0	0	0	8	0	0
78/L-27	13	1	1	0	1	10	1	0
79/L-28	10	6	1	0	3	27	4	0
80/L-29	3	21	9	0	1	12	5	0
84/L-31	7	0	0	0	12	22	1	0
85/L-32	31	1	0	0	1	44	10	0
87/L-33	9	8	0	0	9	39	4	0
88/L-34	114	1	0	0	87	60	0	0
89/L-35	10	4	4	0	6	22	8	0
90/L-36	0	0	0	0	0	7	3	0
91/L-37	2	0	0	0	2	17	1	0
94/L-38	5	12	1	0	2	16	4	0
HC_1526	0	0	0	0	0	5	2	0
HC_1528	6	3	0	0	115	136	7	0
HC_1529	1	3	0	0	98	51	6	0

Table E-3. (Continued)

	MIWSSD				MIWASE			
STATION	1	2	3	4	1	2	3	4
1/L-1	0	0	0	0	0	1	1	0
3/L-2	0	0	0	0	0	1	1	0
4/L-3	0	0	0	0	0	1	0	0
5/L-4	0	0	0	0	2	18	0	0
6/L-5	0	8	6	0	0	2	1	0
8/L-7	0	0	0	1	7	10	12	0
10/L-9	0	0	0	0	0	2	7	0
11/L-10	0	0	0	0	1	0	0	1
12/L-11	0	2	0	0	0	0	1	0
15/L-13	0	0	0	0	4	10	13	1
17/L-14	0	0	0	0	0	2	3	0
19/L-15	1	0	0	0	1	0	2	0
22/L-16	0	0	0	0	0	0	0	0
23/L-17	0	1	1	0	0	1	1	0
24/L-18	1	5	1	0	2	11	17	0
28/L-19	1	0	0	0	2	5	0	0
30/L-20	1	1	0	0	1	1	3	0
36/L-22	0	0	1	0	0	0	1	0
38/L-23	0	0	0	0	0	1	1	0
39/L-24	2	0	0	0	0	0	3	0
40/L-25	2	5	0	0	0	3	1	0
41/L-26	0	0	0	0	0	1	8	0
78/L-27	3	1	0	0	0	5	3	1
79/L-28	3	0	0	0	5	29	11	0
80/L-29	2	5	1	0	0	4	1	0
84/L-31	0	0	0	0	0	1	3	0
85/L-32	0	0	0	0	0	6	4	0
87/L-33	0	1	1	0	0	0	5	0
88/L-34	0	0	0	0	11	5	2	0
89/L-35	0	0	0	0	3	19	6	2
90/L-36	0	0	0	0	0	0	0	0
91/L-37	0	0	0	0	8	2	1	0
94/L-38	0	0	0	0	3	5	2	0
HC_1526	1	0	0	0	0	0	1	0
HC_1528	13	3	0	0	35	17	2	0
HC_1529	4	0	0	0	2	9	4	1

Table E-3. (Continued)

	MISRSE				MISBSE			
STATION	1	2	3	4	1	2	3	4
1/L-1	0	0	0	0	0	0	0	0
3/L-2	0	0	0	0	0	0	0	0
4/L-3	1	15	2	0	0	0	0	0
5/L-4	0	0	0	0	0	0	0	0
6/L-5	0	1	0	0	0	0	0	0
8/L-7	1	22	2	0	5	19	0	0
10/L-9	5	27	12	0	9	30	2	1
11/L-10	0	0	0	0	17	46	0	0
12/L-11	1	3	2	2	1	1	0	0
15/L-13	0	2	1	1	45	45	1	0
17/L-14	0	0	0	2	10	27	1	0
19/L-15	0	5	1	0	6	17	0	0
22/L-16	1	0	1	0	7	8	0	0
23/L-17	0	20	13	1	1	5	3	0
24/L-18	0	79	29	0	3	6	1	0
28/L-19	0	4	2	1	0	1	0	0
30/L-20	0	0	0	0	0	2	0	0
36/L-22	3	6	10	0	0	0	0	0
38/L-23	0	0	3	2	0	1	0	0
39/L-24	0	39	0	0	0	0	0	0
40/L-25	0	11	1	0	1	2	1	0
41/L-26	0	2	2	0	2	0	0	0
78/L-27	3	6	2	0	5	5	4	0
79/L-28	1	55	7	0	8	5	0	0
80/L-29	13	78	2	0	1	16	5	0
84/L-31	0	4	1	1	9	20	6	0
85/L-32	0	9	5	0	20	17	3	0
87/L-33	1	31	1	0	9	9	1	0
88/L-34	5	3	0	1	138	40	0	0
89/L-35	1	14	22	4	21	16	4	0
90/L-36	0	2	0	0	0	16	1	0
91/L-37	2	40	3	0	14	27	3	0
94/L-38	4	66	12	0	0	4	3	0
HC_1526	1	1	1	0	0	0	0	0
HC_1528	2	2	1	0	2	8	0	0
HC_1529	0	0	0	0	2	1	0	0

Table E-4. Absolute frequencies of benthic polychaetes per station in each attribute (families) of the taxonomic approach. Attribute code represents the first five characters of the family name.

STATION	DEPTH	AMPHA	APIST	ARENI	CAPIT	CHAET	CIRRA	COSSU	DORVI	EUCIN
1/L-1	594	0	1	0	0	0	5	0	0	0
3/L-2	618	2	0	0	0	0	1	0	0	0
4/L-3	385	0	0	0	0	1	0	0	0	0
5/L-4	438	0	0	0	0	0	0	0	0	1
6/L-5	318	0	0	0	0	0	0	0	0	0
8/L-7	128	2	0	0	0	0	21	0	1	0
10/L-9	183	0	1	0	0	0	39	0	0	0
11/L-10	183	0	1	1	0	0	10	3	0	0
12/L-11	128	0	0	0	0	0	34	2	0	0
15/L-13	155	6	2	0	2	0	9	2	1	0
17/L-14	144	1	0	0	1	0	26	1	0	0
19/L-15	164	0	0	0	0	0	16	1	0	0
22/L-16	165	0	0	0	0	0	19	4	0	0
23/L-17	237	1	0	0	2	0	17	3	0	0
24/L-18	146	1	0	0	0	0	31	0	1	0
28/L-19	157	3	0	0	0	0	35	0	0	0
30/L-20	136	1	0	0	13	0	18	0	0	0
36/L-22	420	0	0	0	4	0	16	6	0	0
38/L-23	622	0	0	0	0	0	1	0	0	0
39/L-24	135	0	0	0	1	0	11	0	0	0
40/L-25	85	0	0	0	1	0	1	0	0	0
41/L-26	560	0	0	0	0	0	8	0	0	0
78/L-27	109	0	0	0	0	0	11	0	0	0
79/L-28	164	19	4	0	6	0	23	0	0	0
80/L-29	255	0	1	0	0	0	14	0	1	0
84/L-31	220	1	1	0	0	0	34	2	0	0
85/L-32	152	1	0	0	4	0	55	0	2	0
87/L-33	219	0	1	0	0	0	45	0	0	0
88/L-34	140	3	1	0	8	0	135	21	2	0
89/L-35	285	0	1	0	2	0	30	2	2	0
90/L-36	166	0	0	0	0	0	10	0	0	0
91/L-37	201	1	15	0	0	0	5	0	0	0
94/L-38	225	2	6	0	4	0	15	0	0	0
HC_1526	375	1	0	0	1	0	0	0	0	0
HC_1528	330	4	1	0	72	0	245	8	2	0
HC_1529	305	16	0	0	42	0	147	10	1	0

Table E-4. (Continued)

STATION	FLABE	GLYCE	GONIA	LUMBR	MALDA	NEPHT	NEREI	ONUPH	OPHEL	ORBIN
1/L-1	0	0	0	0	0	0	0	1	0	3
3/L-2	0	1	1	0	0	0	0	0	0	0
4/L-3	0	0	0	1	18	0	0	2	0	0
5/L-4	0	3	0	0	0	0	1	0	0	0
6/L-5	0	0	0	1	1	0	0	0	0	0
8/L-7	0	2	0	5	16	3	0	5	0	4
10/L-9	1	1	0	0	28	5	0	0	1	12
11/L-10	0	0	0	0	0	39	0	0	0	7
12/L-11	0	0	0	1	6	6	0	0	0	0
15/L-13	1	0	0	0	4	212	2	1	1	3
17/L-14	0	0	0	0	2	62	0	0	0	1
19/L-15	6	0	0	4	5	102	0	182	0	4
22/L-16	0	0	0	1	2	6	0	0	2	16
23/L-17	0	0	0	1	34	1	0	0	0	1
24/L-18	0	12	0	0	104	26	0	7	10	15
28/L-19	0	3	0	1	4	2	0	174	12	5
30/L-20	0	0	0	0	0	0	5	0	0	7
36/L-22	3	2	0	10	19	0	1	0	0	3
38/L-23	0	1	0	0	5	0	0	6	0	0
39/L-24	0	3	0	0	39	0	0	61	1	0
40/L-25	0	1	0	0	12	1	1	0	0	0
41/L-26	0	0	0	4	4	1	0	0	0	4
78/L-27	0	4	0	0	7	0	0	3	0	1
79/L-28	0	8	0	2	63	3	0	67	0	8
80/L-29	1	8	0	2	84	0	0	13	3	10
84/L-31	0	0	0	8	2	22	0	0	0	8
85/L-32	0	5	0	0	14	7	0	0	1	3
87/L-33	0	8	0	6	33	42	0	141	3	0
88/L-34	9	4	0	1	9	97	0	2	59	8
89/L-35	0	5	0	18	41	26	0	3	2	4
90/L-36	0	0	0	0	2	16	0	0	0	0
91/L-37	0	0	0	0	30	11	0	41	3	9
94/L-38	0	0	0	0	53	1	0	5	25	3
HC_1526	7	1	0	16	1	0	0	1	0	0
HC_1528	10	4	0	104	5	0	1	5	4	0
HC_1529	8	1	0	72	0	0	2	0	2	1

Table E-4. (Continued)

STATION	OWENI	PARAO	PECTI	PHYLL	PILAR	POLYN	SABEL	SCALI	SERPU	SIGAL
1/L-1	0	0	0	0	0	1	0	0	0	0
3/L-2	0	0	0	0	0	0	0	0	0	0
4/L-3	0	2	0	0	0	0	0	0	0	0
5/L-4	0	1	0	0	0	0	3	0	0	0
6/L-5	0	0	0	0	0	0	15	0	0	0
8/L-7	19	1	0	19	0	4	45	1	0	0
10/L-9	19	50	1	7	0	5	7	1	0	0
11/L-10	0	31	0	5	0	0	31	0	0	0
12/L-11	2	13	0	2	0	0	11	0	2	0
15/L-13	14	5	14	13	0	1	168	0	0	0
17/L-14	0	17	1	20	0	4	20	0	0	0
19/L-15	1	6	4	12	0	6	3	1	0	1
22/L-16	0	39	0	20	0	2	15	0	0	0
23/L-17	0	23	0	4	0	3	3	1	1	0
24/L-18	9	32	0	10	0	7	24	0	6	0
28/L-19	7	12	2	4	0	4	2	4	1	0
30/L-20	0	6	0	3	0	12	0	0	2	0
36/L-22	0	40	0	2	1	1	2	0	0	0
38/L-23	0	1	0	0	1	0	9	0	0	1
39/L-24	0	35	0	3	0	1	3	0	0	0
40/L-25	1	1	0	0	0	2	2	0	5	0
41/L-26	0	3	0	0	0	0	0	0	0	0
78/L-27	4	17	0	4	0	2	15	1	4	0
79/L-28	1	20	0	6	0	2	17	2	3	0
80/L-29	13	105	1	6	0	1	38	0	3	0
84/L-31	4	18	2	17	0	1	7	0	0	0
85/L-32	1	20	0	6	0	4	32	2	0	0
87/L-33	0	97	0	13	0	3	19	0	0	0
88/L-34	0	93	2	18	0	45	115	4	0	0
89/L-35	5	53	0	5	0	1	18	7	0	0
90/L-36	0	11	0	6	0	0	0	0	0	0
91/L-37	24	26	1	7	2	2	2	3	0	0
94/L-38	36	19	0	3	0	2	18	1	0	0
HC_1526	2	0	0	0	0	5	1	0	0	0
HC_1528	0	21	0	2	0	22	25	2	0	0
HC_1529	0	15	0	0	0	12	8	0	0	0

Table E-4. (Continued)

STATION	SPHAE	SPION	SYLLI	TEREB	TRICH	TROCH
1/L-1	0	0	1	2	0	0
3/L-2	0	0	0	0	0	0
4/L-3	0	0	0	0	0	0
5/L-4	0	0	2	19	2	0
6/L-5	0	0	0	3	0	0
8/L-7	0	24	2	12	6	0
10/L-9	0	42	7	5	1	2
11/L-10	0	63	0	2	0	1
12/L-11	1	2	0	1	0	0
15/L-13	1	91	1	8	0	0
17/L-14	0	38	1	1	3	0
19/L-15	3	23	10	1	2	4
22/L-16	0	15	4	0	0	0
23/L-17	0	9	1	0	1	2
24/L-18	0	10	7	6	19	13
28/L-19	0	1	18	0	0	1
30/L-20	0	2	3	4	0	0
36/L-22	0	0	6	1	0	0
38/L-23	0	1	0	2	0	0
39/L-24	0	0	14	2	1	0
40/L-25	0	4	10	5	0	0
41/L-26	0	2	0	9	0	0
78/L-27	0	14	20	10	0	0
79/L-28	0	13	33	31	1	0
80/L-29	3	22	6	3	0	0
84/L-31	2	35	1	3	0	0
85/L-32	1	40	22	8	0	0
87/L-33	0	19	3	10	1	0
88/L-34	7	178	109	17	0	0
89/L-35	0	41	3	29	1	0
90/L-36	0	17	3	0	0	0
91/L-37	0	44	3	1	0	0
94/L-38	0	7	2	2	0	0
HC_1526	0	0	2	0	0	0
HC_1528	0	10	26	50	2	0
HC_1529	1	3	17	0	0	0

Appendix F

Total number of individuals per foraging mode for each polychaete family

Table F-1. Total number of individuals per foraging mode in each polychaete family from the Labrador continental shelf and slope and Hermitage Channel. See text and and Figure 2 for explanation of codes for foraging modes.

FAMILY	FORAGING MODE									
	MASRMO	MASRDM	MISRMO	MISBMO	MIWADM	MISRDM	MIWASE	MISRSE	MISBSE	MIWSSD
Ampharetidae	0	0	0	0	0	0	0	65	0	0
Apistobranchidae	0	0	0	0	0	36	0	0	0	0
Arenicolidae	0	0	0	0	0	1	0	0	0	0
Capitellidae	0	0	53	110	0	0	0	0	0	0
Chaetopteridae	0	0	0	0	0	0	0	1	0	0
Cirratulidae	0	0	15	0	0	1072	0	0	0	0
Cossuridae	0	0	0	65	0	0	0	0	0	0
Dorvilleidae	7	0	6	0	0	0	0	0	0	0
Eucinidae	0	1	0	0	0	0	0	0	0	0
Flabelligeridae	0	0	3	0	0	43	0	0	0	0
Glyceridae	0	77	0	0	0	0	0	0	0	0
Goniadidae	0	1	0	0	0	0	0	0	0	0
Lumbrineridae	257	0	1	0	0	0	0	0	0	0
Maldanidae	0	0	0	0	0	0	0	0	647	0
Nephtyidae	691	0	0	0	0	0	0	0	0	0
Nereidae	13	0	0	0	0	0	0	0	0	0
Onuphidae	720	0	0	0	0	0	0	0	0	0
Opheliidae	0	0	0	129	0	0	0	0	0	0
Orbiniidae	0	0	0	140	0	0	0	0	0	0
Oweniidae	0	0	0	0	0	0	0	0	98	64
Paraonidae	0	0	833	0	0	0	0	0	0	0
Pectinidae	0	0	0	28	0	0	0	0	0	0
Phyllodocidae	217	0	0	0	0	0	0	0	0	0
Pilargiidae	4	0	0	0	0	0	0	0	0	0
Polynoidae	155	0	0	0	0	0	0	0	0	0
Sabellidae	0	0	0	0	627	0	51	0	0	0
Scalibregmidae	0	0	0	30	0	0	0	0	0	0
Serpulidae	0	0	0	0	0	0	27	0	0	0
Sigalionidae	2	0	0	0	0	0	0	0	0	0
Sphaerodoridae	0	0	0	19	0	0	0	0	0	0
Spionidae	0	0	0	0	0	0	0	0	0	770
Syllidae	337	0	0	0	0	0	0	0	0	0
Terebellidae	0	0	0	0	0	31	0	216	0	0
Trichobranchidae	0	0	0	0	0	0	0	40	0	0
Trochochaetidae	0	0	0	0	0	23	0	0	0	0