A SURVEY OF THE INVERTEBRATE COMMUNITIES IN THE LITTORAL ZONES OF FOUR LAKES IN THE UPPER PENINSULA OF MICHIGAN: THE POSSIBLE CASCADING TROPHIC INTERACTIONS IN THE INVERTEBRATE COMMUNITIES OF THE LITTORAL ZONE

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ABSTRACT

Four Lakes, Peter, Paul East and West Long, were all sampled using an Ekman grab to determine the composition of the invertebrate communities in the littoral zone. These samples were taken from each lake during three sampling periods over the course of the summer.

The invertebrate communities were analyzed at the level of order except for the Dipterans which were broken up into Chironomids and other Dipterans. The invertebrate communities were compared to see if there were any differences due to the different fish populations. The cascade theory predicts that lakes dominated by piscivorous fish would have large populations of large invertebrates while lakes dominated by smaller fish would tend to have smaller invertebrates due to predation by these fish. From my results, there is some evidence of a cascade effect although the results do not completely support the cascade theory. The lack of strong evidence for the cascade effect does not mean that it does not have an influence on the invertebrate communities. Variable fish diets, emergences of insects and the influence of other factors could all affect the impact of the cascade effect on the invertebrate communities.

INTRODUCTION

Lake communities are governed by an extremely complex set of interactions between the biotic and abiotic factors of the system.

Ecosystem processes can be described by both bottom-up and top-down interactions. Bottom-up descriptions show how nutrients move up the food chain from producers to higher order consumers. Producers are the base of the food web. These organisms use nutrients and carbon dioxide along with light energy from the sun to produce energy and biomass. The producers are then eaten by primary consumers which cannot themselves produce food or energy. These are then eaten by secondary consumers and so on. The amount of biomass which the producers accumulate limits the amount of biomass which the secondary consumers can accumulate. This, in turn, limits the amount of biomass which the secondary consumers can accumulate and so on up the food chain (Carpenter, 1988).

Top-down descriptions of ecosystem processes show how predation by higher order consumers can limit the populations of lower order consumers and producers. Top-down interactions are referred to as cascading trophic interactions because predation by higher order consumers can directly and indirectly affect the populations of lower order consumers and producers. One possible though very simplistic example is a lake dominated by piscivorous fish. These fish limit the numbers of smaller fish which feed on large invertebrates. The reduced population of smaller fish allows the populations of larger invertebrates to increase. The large invertebrates, which are often predatory, limit the populations of smaller invertebrates which feed on phytoplankton. The

small populations of small invertebrates are unable to limit the phytoplankton which increases and reduces the amount of light available to the macrophytes (Carpenter, 1988). The reduced light in turn limits macrophyte production.

Another possible example is a lake dominated by smaller fish. These limit the populations of large invertebrates allowing for a subsequent increase in the populations of smaller invertebrates (Carpenter, 1988). The large populations of small invertebrates reduce the amount of phytoplankton in the lake allowing for more light to reach the macrophytes which can produce and accumulate biomass.

These are extremely oversimplified and highly theoretical examples of the cascade effect. However, the cascade effect has been shown to be a significant factor in determining the structure of invertebrate communities of the pelagic (open-water) zone of lakes (Carpenter et al., 1987). Stein et al. (1988) and Crowder et al. (1988) suggest that fish predation in the pelagic zone limits the populations of larger and slower invertebrates. Crowder and Cooper (1982) found that bluegill (*Lepomis macrochirus*) reduced the numbers of large invertebrates such as Odonates and *Hyalella* in experimental ponds. However, the importance of the cascade effect in determining the invertebrate community of the littoral (near-shore) zone of lakes has not yet been explored in whole lake manipulations. In this paper, I examine the invertebrate communities of four lakes in the Upper Peninsula of MIchigan. From this information and from the known fish populations of each lake, I will examine possible cascade effects between the fish and invertebrates of each lake.

From knowledge of the fish populations and the cascade theory, one

could make several predictions about each lake. Peter lake is stocked with golden shiners, northern redbelly dace, finescale dace central mudminnows and a few largemouth bass and rainbow trout. The minnows feed primarily on microcrustaceans such as cladocerans and copepods (Becker, 1983). One could predict from this information that their impact upon the invertebrate communities of the littoral zone would be negligible as there are few microcrustaceans in the littoral zone. Paul is dominated by largemouth bass which tend to be piscivorous (Becker, 1983). East and West Long are both dominated by yellow perch and smallmouth bass. Yellow perch are omnivores while smallmouth bass tend to be piscivores (Becker, 1983). However, Becker (1983) also states that these fish can have widely varied diets. All three fish will readily feed upon large invertebrates especially Odonates. From this information we could predict that the predation pressure on large invertebrates in the littoral zone would be highest in East and West Long Lakes and lowest in Peter Lake while predation pressure in Paul would have an intermediate amount of predation pressure. Those organisms which would be most vulnerable to predation by fish would be those organisms which are large enough to be obvious to potential predators and which do not burrow into the sediments. This hypothesis has been supported by several studies (Crowder et al., 1988, Stein et al., 1988, Mittelbach, 1988, and Post and Cucin, 1984). The invertebrates which would meet these requirements would include Odonates, Ephemeropterans, Trichopterans, Amphipods and Hirudinea. Chironomids, while being by far the most abundant organisms of the littoral community, are smaller and usually buried in the sediments and so are probably not exposed to the direct effects of fish predation

MATERIALS AND METHODS

A. Study Sites

Peter, Paul and Long Lakes are all seepage lakes located on the University of Notre Dame Environmental Research Center in Gogebic County in the Upper Peninsula of Michigan. Peter and Paul were one lake until they were divided in 1951. Prior to 1951, the lakes were dominated by largemouth bass (Micropterus salmoides). After 1951, both lakes were subjected to several manipulations including the addition of lime (CaCO₃) and several manipulations of the fish populations. In both lakes, the populations of largemouth bass recovered by about 1975 (Leavitt, Unpublished). Since then, attempts have been made to remove the largemouth bass from Peter Lake and replace them with redbelly dace (*Phoxinus eos*), finescale dace (Phoxinus neogaeus), and central mudminnows (Umbra limi) (Carpenter et al., 1987). By 1987, the bass populations had recovered. In 1989, Rainbow trout were added to the lake and in the spring of 1990, 20,000 golden shiners were added to Peter Lake. Both lakes have steep gradients which reach depths of 12.2 m in Paul Lake and 19.3 m in Peter Lake. Peter Lake covers approximately 6.0 acres and has a total volume of 436x10³ m³. Paul Lake covers an area of 3.0 acres and has a total volume of 134x10³ m³ (Ehrman, 1989).

Long Lake is a dumbell-shaped lake with a basin at each end. Plans are currently under way to isolate each basin with a rubber curtain so that whole lake manipulations may be done on Long Lake. For this reason, Long Lake will be treated here as two lakes, East and West Long Lakes. Both lakes are stocked primarily with smallmouth bass (*Micropterus dolomieui*)

and yellow perch (*Perca flavescens*). Both basins have gentler gradients than Peter or Paul Lakes and both reach a maximum depth of about 14 meters (Ehrman, 1989).

B. Sampling

All sampling was done using a 0.003 m³ Ekman grab. Seven grabs were removed from each lake during each of three sampling periods. All lakes were sampled on June 11,1990 and July 9, 1990. During the third sampling period, East Long was sampled on July 28, 1990, West Long was sampled on on July 29, 1990, and Peter and Paul were both sampled on July 31, 1990. To insure that the lakes were thoroughly sampled and that sampling was done randomly, each lake was divided into seven sectors. Each sector was then divided into ten segments. One segment was randomly chosen for each sector and for each sampling period and sampling was done in that segment. All samples were taken from a depth of 1.0 m which is the approximate midpoint of the epilimnion of each lake.

After the samples were taken, they were rinsed in a 0.595 mm sieve out in the field. The sediments were then placed in plastic bags and taken back to the laboratory. The samples were put in a refrigerator until they could be processed. All insects were collected by sucrose flotation (300g/L). After collecting all the insects, the sugar water was filtered out and the sediments were examined in an enamel pan using forceps and a probe to collect the bivalves. All organisms collected were preserved in 70% ethanol and identified to genus except for most of the Dipterans which were identified to the level of family. The Dipterans from Peter Lake during the first sampling period were identified to the level of genus. The

insects were identified using the dichotomous keys of Hilsenhoff (Undated) and Merritt and Cummings (1978). The non-insect invertebrates were identified using the dichotomous keys of Pennak (1953). These were then grouped into functional feeding groups using the classification system of Merritt and Cummings (1978).

RESULTS

The mean number of invertebrates per square meter in each lake during each sampling period is shown in Figure 1. The taxa common to each lake were Odonata, Ephemeroptera, Trichoptera, Megaloptera, Diptera and Bivalva. The Odonata present were predominantly Ladona (Libellulidae), Epitheca Corduliidae and Stylurus (Gomphidae). The Ephemeroptera were almost entirely Caenis (Caenidae) while the Megaloptera were exclusively Sialis (Sialidae). The Trichoptera found included Polycentropus (Polycentropodidae), Molannus Molannidae and Limnephilidae which were not identified to genus. The Dipterans were predominantly Chironomidae although Ceratopogonidae were common in each lake. Figures 2 and 3 show how the percent abundance of each order changed over time in each lake. Figures four through six are bar graphs which also show percent abundance of each order during each sampling period.

Figures eleven through thirteen are bar graphs of the percent abundance of each functional feeding group for each sampling period. The feeding groups are those of Merritt and Cummins (1978). Piercers and shredders are both predators which use different methods of feeding. These include Odonates, Polycentropodidae and Megalopterans (engulfers) and Hemipterans (piercers). Shredders, collectors and scrapers are all detritivores and herbivores. These include Limnephilidae (shredders and some scrapers) and Ephemeropterans (collectors). Bivalves were included under filterers and those taxa which were not specific enough to be grouped under a specific functional group were included under "Other." This group includes all Chironomidae which need to be identified to genus

to be grouped in a functional feeding group.

Figure seven shows the total number of vulnerable taxa. The vulnerable taxa are those which would be most likely to be affected by predation pressure due to their relative sizes and habits. The large, free-swimming organisms would be most likely to be affected by fish predation. The vulnerable taxa include Odonates, Ephemeropterans, Trichopterans (divided into Polycentropodids and Limnephilids for analysis), Amphipods and Hirudinea. Figures eight through ten show the absolute abundances of each of these taxa during each of the three sampling periods.

During the first sampling period, there were nine total Odonates in Peter, five in Paul, six in East Long and seven in West Long. Of those Odonates in East Long, two are of the family Gomphidae which are burrowers and would probably not be exposed to predation. Also, two of the Odonates in West Long were Gomphids.

During the second sampling period, there were five Odonates in Peter, one in Paul, six in East Long and ten in West Long. Of the Odonates in West Long, four were Gomphids.

During the last sampling period, Peter had six Odonates, Paul had no Odonates, East Long had fourteen Odonates and West Long had eleven Odonates. Peter had one Gomphidae, East Long had one Gomphidae and West Long had two Gomphidae.

Another Order which would be vulnerable to predation by fish would be the Order Ephemeroptera. During the first sampling period, Peter had eleven total Ephemeroptera, Paul had six, East Long had four and West Long had eight. During the second sampling period, Peter had ninety-five total

Ephemeropterans, Paul had eighty-eight, East had two and West had two.

During the last sampling period, Peter had fifteen total Ephemeropterans,

Paul had forty-three and East and West Long each had three.

The Trichopterans were divided into Polycentropodidae and Limnephilidae for the analysis. The Polycentropodids are free swimming caddis-flies while the Limnephilids are case builders. Peter had three Limnephilids and four Polycentropodids while Paul had thirteen Limnephilids and two Polycentropodids. East Long and West Long both had four Limnephilids and neither lake had any Polycentropodids. During the second sampling period, however, the number of Polycentropodids increased significantly in East Long and West Long. East Long had twenty-seven Polycentropodids while West Long had sixteen. Peter again had twice as many Polycentropodids as Paul with seven while Paul only had three. For the Limnephilids, Peter had no Limnephilids while Paul had eight. East Long had five Limnephilids while West Long had one. During the third sampling period, Peter had twelve Polycentropodids and seven Limnephilids while Paul had three Polycentropodids and seven Limnephilids. East Long had twenty-three Polycentropodids and twelve Limnephilids while West Long had fifteen Polycentropodids and six Limnephilids.

For the Amphipods, Peter had the lowest during the first and second sampling periods with no Amphipods during either sampling period. Peter had four Amphipods during the last sampling period. Paul had three Amphipods during the June sampling, sixteen during July and eight during August. East Long had two Amphipods in the June sampling period, one in July and two in August. For West Long, the number of Amphipods was

seventeen during the June sampling period, zero for July and two for the August sampling period.

The Hirudinea are the last organisms which would be to predation.

During the June sampling period, one Hirudinea was found in East Long.

During July, two Hirudinea were found in Peter and two in Paul. During the last sampling period, one leech was found in Peter and one in Paul.

DISCUSSION

Looking at the vulnerable taxa, there does seem to be some evidence of a cascade effect. Figure seven shows that during the July sampling period, the total number of vulnerable taxa in Peter and Paul is more than twice the number in East and West Long. This lends strong support to the cascade theory since the cascade theory would predict that predation would be highest in East and West Long due to the presence of smallmouth bass and yellow perch. However, this evidence is lacking in the June and August sampling period and reasons for this will be discussed later.

The Odonates do seem to affected to some degree if one compares the data from Peter and Paul. Peter would be expected to have the less predation pressure than Paul due to the presence of largemouth bass in Paul. This is indeed the case as Peter has a higher number of Odonates than Paul in all three sampling periods. However, East and West Long would be expected to have the highest predation pressure of all the lakes and this is not the case during any sampling period.

The Ephemeropterans appear to be extremely vulnerable to the effects of predation. During the first sampling period, there is little difference in the number of Ephemeropterans in each lake. However, during the last two sampling periods, the number of Ephemeropterans in Peter and Paul increased dramatically while it decreased in East and West Long.

Apparently, the predation by the smallmouth bass and yellow perch was extremely heavy in East and West Long. This resulted in dramatic differences in the number of Ephemeropterans in Peter and Paul Lakes and East and West Long Lakes.

The Trichopterans are the third group of invertebrates which are vulnerable to predation. These were further divided into Polycentropodidae and Limnephilidae. The Polycentropodids would be expected to have a high degree of predation pressure as they are free swimming organisms. As with the Odonates, there is some evidence for this in comparing Peter and Paul. Peter has higher numbers of Polycentropodids during all three sampling periods. However, predation pressure would be expected to be the highest in East and West Long and this is clearly not the case. During the second and third sampling periods, East and West Long each have higher numbers of Polycentropodids than either Peter or Paul. The Post and Cucin (1984) found that the introduction of yellow perch significantly reduced the densities of Trichopterans. However, this clearly does not seem to be the case with the Polycentropodids in these lakes.

The Limnephilids do not seem to show much evidence of predation pressure. Peter had the lowest number of Limnephilids during the first two sampling periods and the second lowest number of Limnephilids during the August sampling period. East and West Long show some evidence of predation pressure when compared to Paul but East Long had the highest number of Limnephilids during the third sampling period. It may be that the cases of the Limnephilids offer them some degree of protection from predation.

The Amphipods do seem to show some evidence of a cascade effect. Since these are small, fast crustaceans, predation by the larger fish such as bass and perch would probably be minimal while predation by the golden shiners would be high especially on the smaller Amphipods. This would suggest that the number of Amphipods would be lowest in Peter. This is

the case for both the first and second sampling periods as Peter had no Amphipods in either sampling period. However, Peter had more Amphipods than East Long and West Long in the third sampling period. This seems to suggest that the cascade effect has had some influence in the populations of Amphipods. The Hirudinea (leeches) are the last group which would be vulnerable to the effects of fish predation. Peter and Paul had the highest total number of Hirudinea but the low number of leeches collected prevents an adequate analysis of cascade effects on this Order.

Overall, the evidence for a cascade effect is limited especially since no statistics were used in the analysis. There are several reasons why the cascade effect may not appear to have a significant effect on the invertebrate populations of the lakes. One reason is that the exact fish populations and the exact fish diets are not known. A small number of largemouth bass would not be able to limit the populations of smaller fish. In addition, the age structure of the fish populations is not known. Adult bass and yellow perch have different diets than young of the year and juvenile fish (Becker, 1983). Also, the exact fish diets are not known and the diets of most of these fish are extremely variable. For example, largemouth bass tend to be predominantly piscivores but they will also feed on invertebrates especially Odonates (Becker, 1983). This could explain the small percentage of Odonates in Paul Lake. Also, Cochran et al. (1988) found that finescale dace, *Phoxinus neogaeus*, fed on high numbers of macroinvertebrates including Dipterans, Odonates, Trichopterans, Coleopterans and Ephemeropterans. This means that even the fish in Peter Lake can have highly variable diets which could further obscure any cascade effects.

Another problem in analyzing the invertebrate community is that nearly all the insects have adult stages which are terrestrial. Since most emergences tend to be within a small period of time, the percentage of a group of insects could drop significantly in a short time due to an emergence of adult insects. This could create significant problems in the analysis if emergences occur at different times in different lakes.

Another problem with using the cascade theory to analyze the invertebrate communities is that other factors are present. Bottom-up effects are probably the most predominant factors. If an organism does not have anything to feed upon or is lacking an essential nutrient, then that organism will not be able to survive. This may account for the small number of crustaceans which could be limited by calcium as all four lakes have soft water and therefore are lacking significant amounts of calcium.

Another reason that the fish may not have an effect upon the invertebrate populations is that invertebrate prey may have responses to predation pressure which obscure the effects of the predation pressure. Predation may cause a shift in distribution of the invertebrates.

Invertebrates may avoid predation by hiding under rocks and snag.

Although no quantitative data was taken, each lake had large amounts of snag habitats which could provide refuge for potential prey.

Another problem with this experiment is that it assumes that the littoral zone is a closed system which means that the fish feed only in the sediments of the littoral zone. However, the fish could also feed upon invertebrates found on macrophytes, in the pelagic zone and in the sediments of the metalimnion and hypolimnion. This means that a shift in fish diets could occur if predation pressures on littoral invertebrates

becomes too great allowing for invertebrate populations to recover. Again, the exact fish diets are not known, so the extent of the effects of dietary shifts of the fish are not known.

One last problem is that density may not be affected by the cascade effect. Post and Cucin found that fish predation had little effect on the densities of invertebrates but did affect the mean weights and the total biomass of the invertebrates (1984). Several other authors also suggest that cascade effects of fish predation results in reduced sizes of invertebrates rather than reduced densities (Crowder et al., 1988, Healey, 1984, Mittelbach, 1988, Stein et al., 1988). In this analysis, only the density of the invertebrates and not the mean weights or biomass is considered. It may be that the cascade effect would be more clearly seen if mean weights and biomass were considered. Clearly, further research is necessary to determine the extent of cascade effects in the littoral zones of lakes.

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FIGURE LEGEND

Figure 1

This is a bar graph showing the mean number of invertebrates per square meter in each lake for each of the three sampling periods.

Figure 2

These graphs show the percentage abundance for seven taxa over the course of the summer in Peter Lake and Paul Lake. The taxa which are included are Chironomidae, Odonata, Ephemeroptera, Trichoptera, Megaloptera, and Bivalva. All other invertebrates are grouped under "Other."

Figure 3

These graphs show the percent abundance for seven taxa over the course of the summer in East Long and West Long Lakes. The taxa which are included are the same as those in Figure 2.

Figure 4

This graph shows the percent abundance of each taxonomic group in each lake during the June sampling period.

Figure 5

This graph shows the percent abundance of each taxonomic group in each lake during the July sampling period.

Figure 6

This graph shows the percent abundance of each taxonomic group in each lake during the August sampling period.

Figure 7

This graph shows the total number of vulnerable prey which were collected in each lake during the course of the summer. The vulnerable taxa include Odonata, Ephemeroptera, Polycentropodidae, Limnephilidae, Amphipoda and Hirudinea.

Figure 8

This graph shows the total number of each taxa of vulnerable prey which were collected in each lake during the June sampling period.

Figure 9

This graph shows the total number of each taxa of vulnerable prey which were collected in each lake during the July sampling period.

Figure 10

This graph shows the total number of each taxa of vulnerable prey which were collected in each lake during the August sampling period.

Figure 11

This graph shows the percent abundance of the functional feeding groups of Merritt and Cummins (1978) for the June sampling period. The feeding groups included are Shredders, Collectors, Scrapers, Piercers

(Predators), Engulfers (Predators), Filterers, and Other.

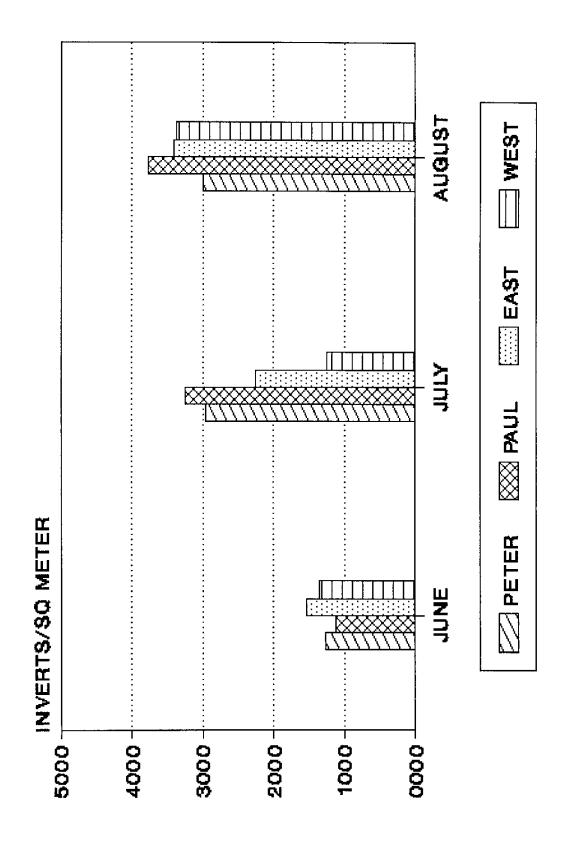
Figure 12

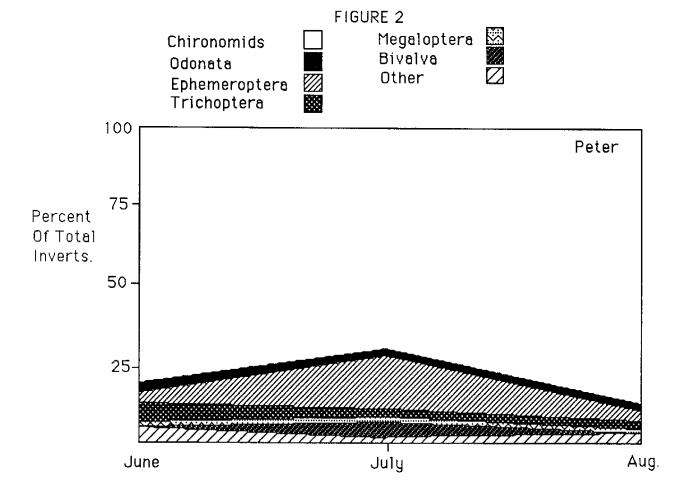
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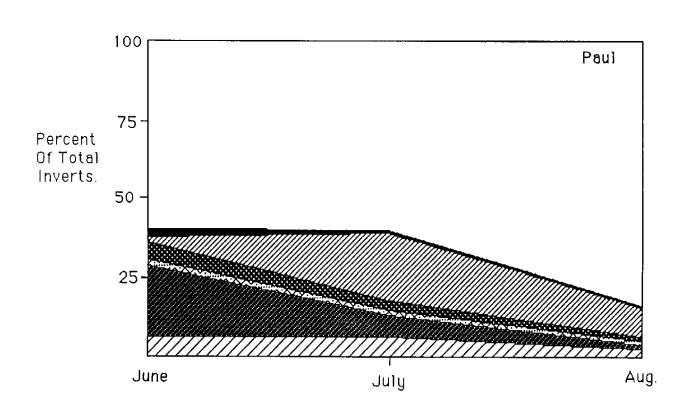
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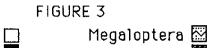
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Figure 1

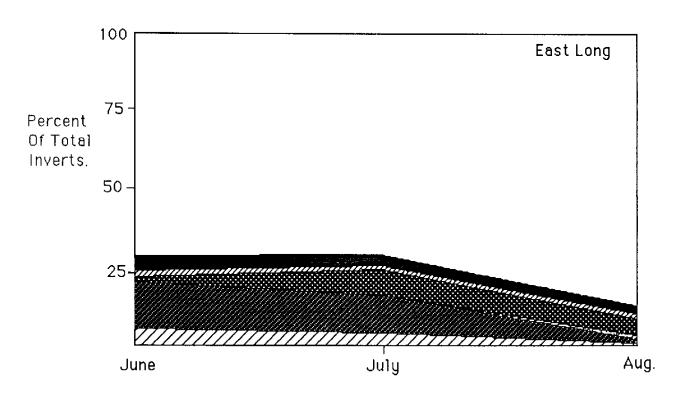


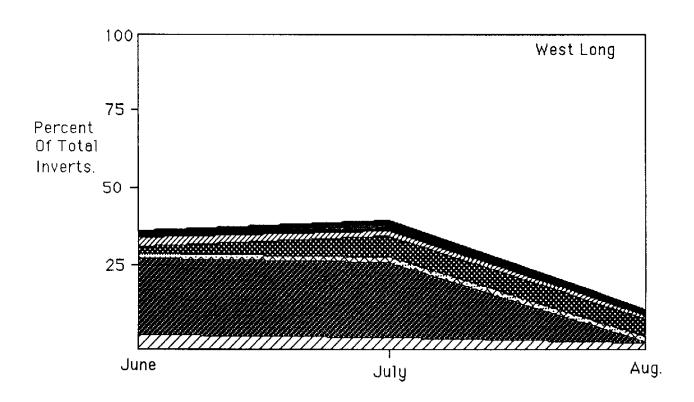




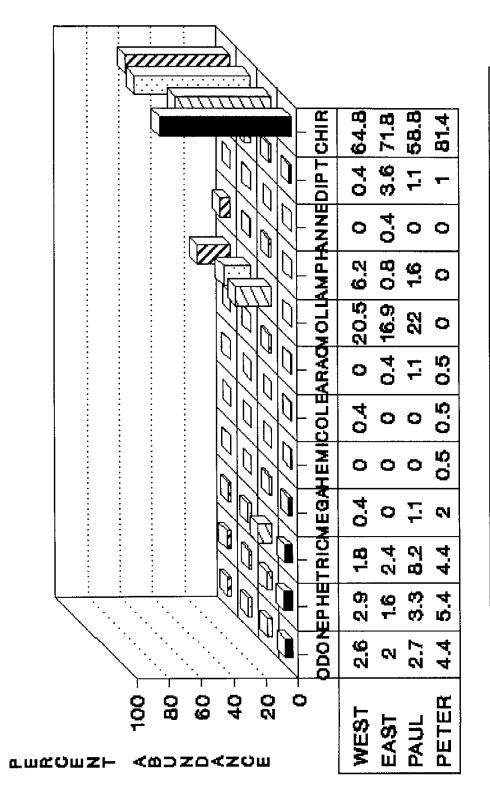






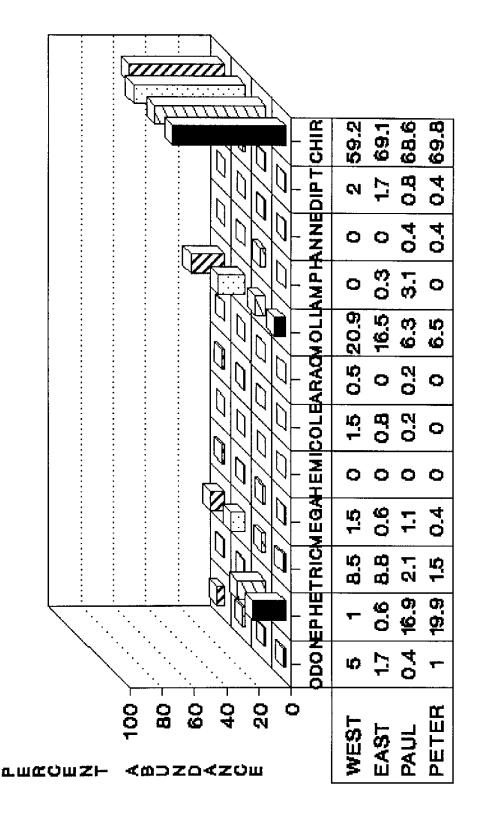


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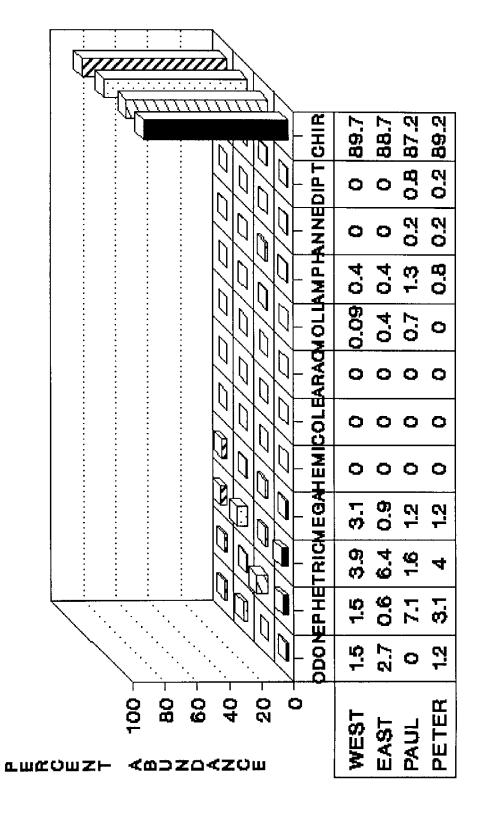
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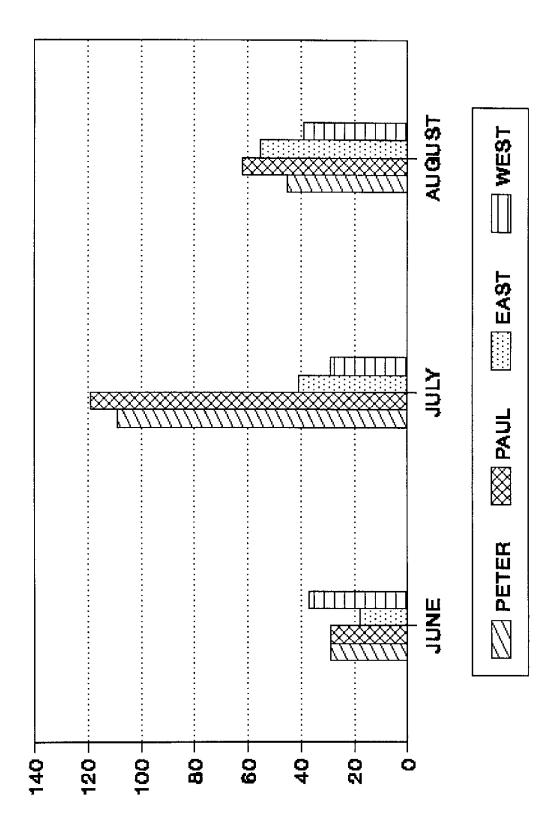
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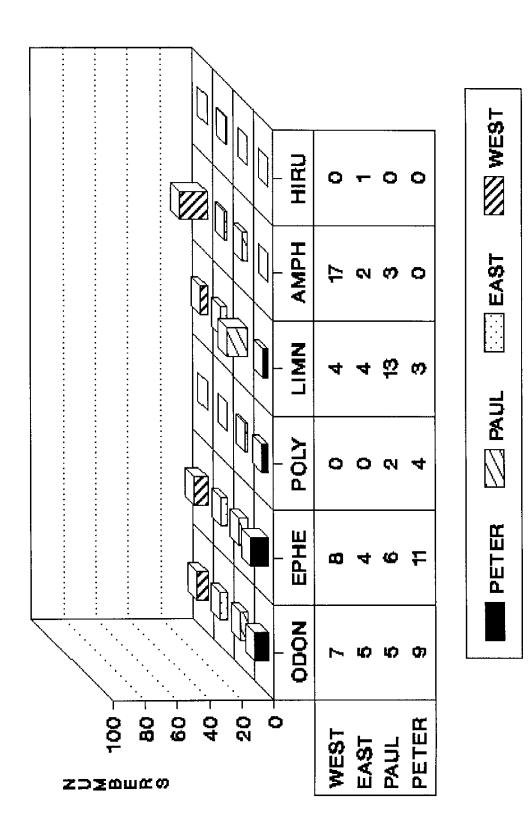


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Figure 7



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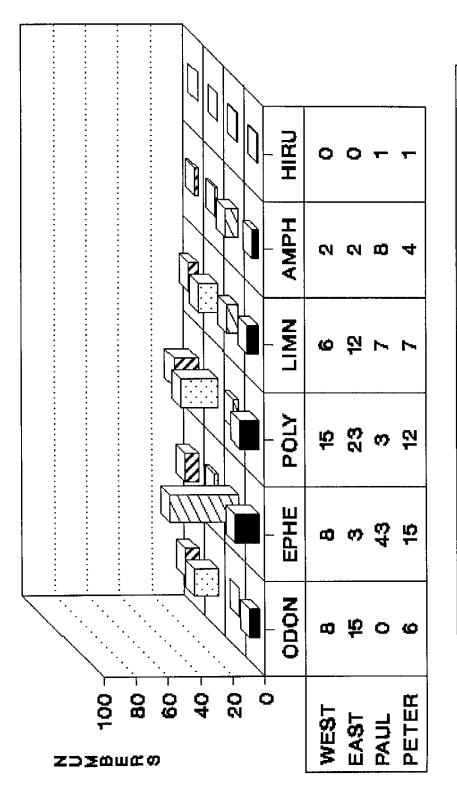
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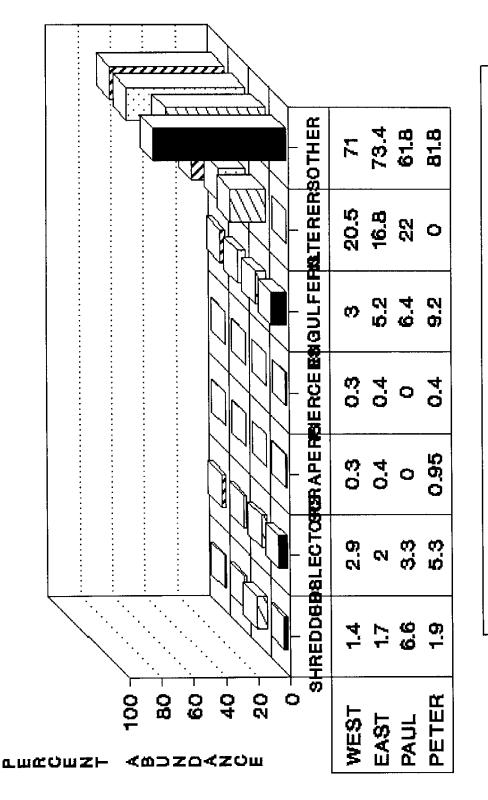
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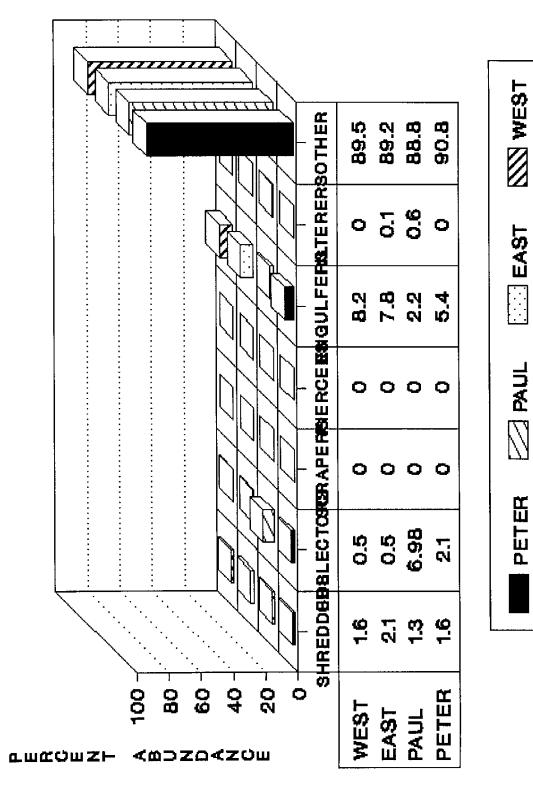
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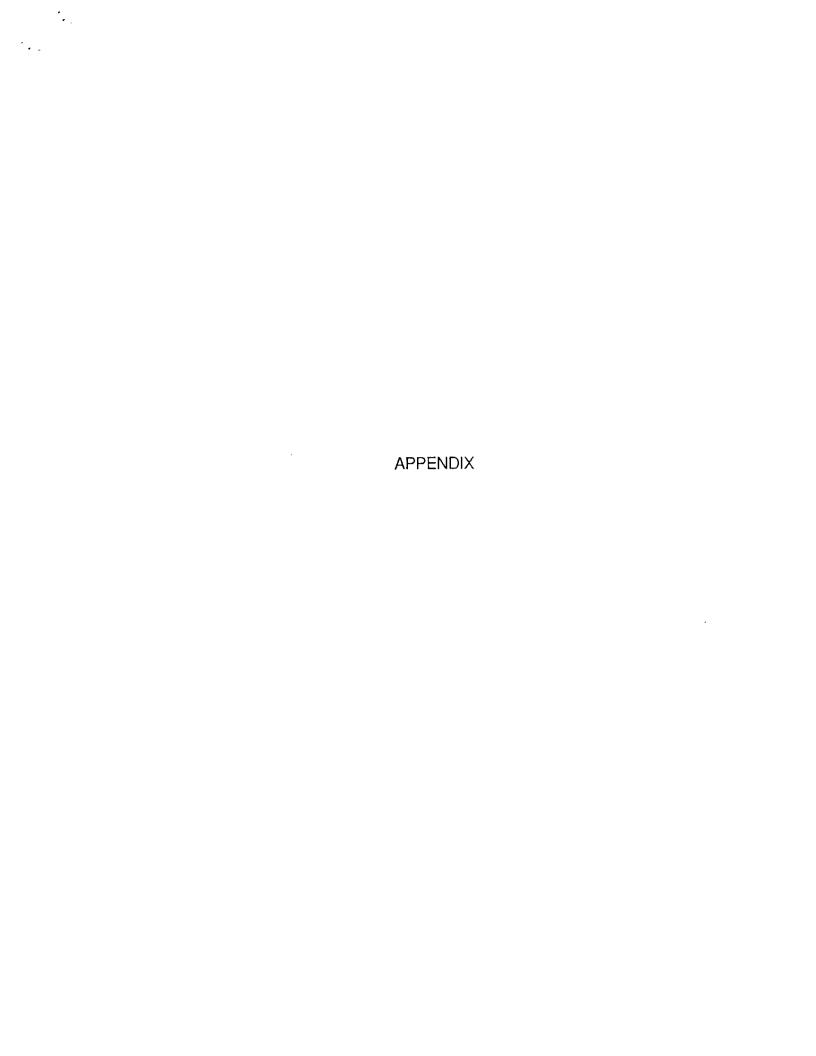
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