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Spatial Patterns Emphasize the Importance of Coastal Zones as Nursery Areas for Larval Walleye in Western Lake Erie

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Abstract

Lake Erie supports the world's largest naturally-reproducing walleye population that, like many natural populations, exhibits significant interannual variability in year-class strength. Recent research revealed the importance of larval vital rates in determining walleye year-class strength in western Lake Erie indicating that spatial overlap of larvae with good habitat conditions (e.g. abundant prey, warm waters) promoted walleye growth and survival. In order to assess the overlap between walleye larvae and associated habitat parameters in western Lake Erie, we evaluated the distribution of walleye larvae with intensive sampling at 30 to 36 sites during spring in 1994-1999. We analyzed the spatial relationships between pelagic walleye larvae and various habitat attributes using a geographic information system and principal components analysis. Larval walleye density was consistently highest at nearshore sites in all years of the study. Larval walleye density was positively associated with zooplankton density, ichthyoplankton density, and water temperature. Walleye density was negatively associated with water depth and secchi disk depth. Two principal components represented 79.6% of the total variability in site attributes. Graphical analysis of principle components scores supported spatial analysis by graphically separating sites into distinct groups based on larval walleye density and habitat attributes. These analyses demonstrated repeatable interannual patterns in larval distribution and habitat attributes emphasizing the importance of coastal zones as nursery areas for walleye.

Introduction

Spatial distribution of fish larvae has proved important in determining their growth and survival as suggested for many marine fishes (Peterman and Bradford 1987; Houde 1987, 1989) and freshwater species in large lakes (Spykerman 1974). Walleye larvae are pelagic and subject to transport by water currents which can dictate their distribution (Houde 1969; Houde and Forney 1970). Laboratory and field studies have shown that larval walleye perform better when exposed to certain habitat conditions. For example, larval walleye growth and survival rates were higher in warmer water temperatures (Hokanson and Koenst 1986, Santucci and Wahl 1993, Clapp et al. 1997), when prey were abundant (Regier and Summerfelt 1999, Trometer and Busch 1999), and in dark water conditions (Bristow et al. 1996, Regier and Summerfelt 1997). Because both larval walleye and good habitat conditions can occur in heterogeneous patches in western Lake Erie, the magnitude of growth and survival can depend on the degree of overlap between larval walleye and habitat. The goal of this study is to identify geographic areas and habitat characteristics important as nursery habitat for pelagic walleye larvae in western Lake Erie and to assess the degree of overlap between larval walleye and specific habitat parameters.

Background

Lake Erie supports the world's largest naturally-reproducing population of walleye with current stock abundance estimates exceeding 40 million adult fish (Lake Erie Walleye Task Group 2000). Lake Erie's walleye population has supported important sport and commercial fisheries in Lake Erie for over 150 years. High exploitation rates coupled with severe water quality and habitat degradation during the first half of the 20th century led to the collapse of the fishery by the early 1960s. The discovery of high levels of mercury in the tissue of walleye prompted closure of the fishery in 1970, offering the exploited population a reprieve from harvest (Regier et al. 1969, Knight 1998). Following the 1972 adoption of the Great Lakes Water Quality Agreement, basin-wide management strategies focused on reducing organic inputs to the lake in efforts to improve fish habitat and rehabilitate populations (Burns 1985, Makarewicz and Bertram 1991). The fishable stock increased from about 83,000 walleye in 1970 to over 14 million in 1976 (Hatch et al. 1987) and landings increased accordingly. Adult population abundance peaked in 1988 when population estimates exceeded 99 million fish age-2 and older. The current population is estimated to exceed 40 million fish (Lake Erie Walleye Task Group 2000).

Despite its large adult population size, the Lake Erie walleye population exhibits wide fluctuations in recruitment. The abundance of age-2 fish entering the stock has varied as much as 60-fold since 1977 (Lake Erie Walleye Task Group 2000). Research conducted in the 1990s concluded that recruitment variability was a consequence of physical processes that influenced early life history stages in spring (Roseman et al. 1996, 1999) and prey abundance during fall that influences spawner physiological condition (Henderson and Nepszy 1994; Madenjian et al. 1996).

In western Lake Erie, walleye spawn on mid-lake reefs in the western basin as well as in tributaries such as the Maumee and Sandusky rivers. Spawning typically begins shortly after ice-out and peaks around the middle of April (Baker and Manz 1971, Roseman et al. 1996). Walleye broadcast their eggs over hard substrates and provide no direct parental protection. Eggs typically hatch in 7 to 15 days depending on water temperature (Hurley 1972, Nepszy et al. 1991, Roseman et al. 1996). In Lake Erie, walleye larvae emerge from the substrate immediately upon hatching and rely on lake currents for transport to nursery areas (Nepszy et al. 1991). The yolk-sac is usually absorbed within 3 to 5 days when the larvae are about 9.5 mm total length (TL). The duration of the pelagic larval stage is temperature dependent and typically lasts from 3 to 4 weeks until the young fish become demersal at about 30 mm TL (McElman and Balon 1979). Due to their small size, limited mobility, and delicate nature, larval walleye are susceptible to a variety of direct and indirect influences from physical processes like water temperature and wind generated currents. These processes can influence the timing and magnitude of larval development, distribution, growth, and survival (Roseman et al. 1999; Roseman 2000).

Study Area

The study area encompasses the area of western Lake Erie located in Ohio waters between latitudes N 41° 30' to N 41° 43' and longitudes W 82° 50' to W 83° 14' (Figure 1). Physical and chemical characteristics of western Lake Erie are well documented (Herderndorf and Braidech 1972; Boyce et al. 1987). The western basin has a mean depth of 7.4 m and a total surface area of about 3,700 km^2. Mean water residence time is about 2.4 months (Burns 1985). Generally, the western basin is isothermal throughout the year due to mixing of its shallow waters and seldom becomes anoxic. Bottom substrates consist primarily of sand and clay, although dolomite limestone forms several major reef complexes (Herdendorf and Braidech 1972).

Methods

Fish Collection

Pelagic ichthyoplankton were sampled once per week from mid April though June at 30-36 sites in Ohio waters of western Lake Erie (Figure 1). We used a 2.0 m^2 framed ichthyoplankton net fitted with 583 μm mesh netting to sample pelagic larval fishes. A flow meter was positioned in the center of the mouth of the net to record the volume of water sampled. The net was towed in the upper 2.0 m of the water column at approximately 1.0 m/sec. for 5 min. Larval fishes were euthanized with a lethal dose of tricaine methanesulfonate and preserved in 95% ethanol. Identifications of larval fish follow Auer (1982). For this analysis we grouped ichthyoplankton species that were of sufficient size to be consumed by age-0 walleye into one group after identification. We present abundance and distribution information on non-walleye ichthyoplankton only for the period when age-0 walleye were piscivorous, which typically began in mid-June based on previous diet studies (Roseman 1997). This group of ichthyoplankton prey consisted of white bass *Morone chrysops*, white perch *Morone americana*, yellow perch *Perca flavescens*, gizzard shad *Dorosoma cepedianum*, spottail shiner *Notropis hudsonius*, emerald shiner *Notropis atherinoides*, and freshwater drum *Aplodinotus grunniens*.

Zooplankton Sampling

From 1996-1999, zooplankton samples were collected at each larval fish sampling site concurrent with fish sampling (Figure 1) during late April, May and early June. This time period covers the time when larval walleye were known to feed on zooplankton

(Roseman 1997). Zooplankton abundance and composition were determined from weekly vertical hauls with a 0.5-m diameter plankton net equipped with 153-μm mesh netting. Samples were immediately preserved in sugar-formalin (Haney and Hall 1973). One to three 1-mL subsamples were withdrawn with a Hensen-Stemple pipette from a known volume of sample. Additional subsamples were counted until at least 150 individual zooplankters had been enumerated. We calculated average numbers per liter for the pooled zooplankton samples collected on each sampling date to show trends in zooplankton abundance. For this analysis, we included only zooplankton taxa known to be consumed by young walleye. Previous diet studies of larval walleye in western Lake Erie showed that pelagic larval walleye consumed mainly copepopds and large cladocerans during April, May and early June (Roseman 1997).

Physical Habitat Characteristic Measurements

Depth was recorded at each sampling site. Because depth increased with distance from shore, we used depth as a surrogate measurement for distance from shore (shallow depths are nearshore). From 1996-1999 we also recorded water temperature 2 m below the water surface at each larval sampling site using a YSI digital temperature meter. We measured water clarity using a Secchi disk (nearest 0.1 m) at each sampling site in all years. We used bottom substrate composition data reported in Fuller (1996) to identify bottom type in our study area.

Data Analysis

To compare larval walleye abundance between years, we calculated a daily mean abundance and standard error for each sampling date. Ichthyoplankton catches from neuston samples were converted to number of larvae/1,000 m^3 of water. We then transformed these catch data to $\log_e (x + 1)$ to produce normalized data with homogeneous variance (O'Gorman 1984) and plotted these against time.

To create graphical representations of geographic patterns in larval fish, zooplankton, water temperature and water clarity across our study area, we used a geographic information system (GIS) to plot the deviations from the overall annual mean values for each attribute at each sampling site as discrete point samples. We used the natural break function in ArcView to group data into distinct categories (Environmental Systems Research Institute 1999). Because larval fish and zooplankton are known to occur in patches of high and low abundance (Patalas and Salki 1992), we treated these data as discrete point samples. For continuity and uniformity in presentation, we treated all attribute data as point samples rather than kriging continuous attributes (temperature and water clarity). We used the sample correlation coefficient (Snedecor and Cochran 1989) to assess relationships between variables.

Principal components analysis (PCA) was used to explore the relationship between variables and demonstrate the relationship between site depth and attribute value. We ran PCA on the site X variable matrix where variables were the deviations from the overall mean values for larval walleye abundance, water depth, water temperature, secchi disk depth, zooplankton abundance, and ichthyoplankton prey abundance for each attribute at each sampling site. Sample sites were categorized into three depth categories with category 1 being shallow nearshore sites (< 3.7 m depth), category 2 being offshore sites with intermediate depth (3.7 – 7 m depth), and category 3 being deep offshore sites (> 7 m depth). We ran one PCA using pooled data from 1996 – 1999. We did not include 1994 and 1995 because the datasets for these years were incomplete. We used the scree diagram method and Joliffe's adaptation of Kaiser's Rule (Jackson 1991) to select principal components for graphical analysis. The scree method allows selection of principal components that are on the steep descending limb of the plot of eigenvalues and Joliffe's adaptation of Kaiser's Rule recommends selecting only those principal components with eigenvalues greater then 0.7 (Jackson 1991). After selecting principal components, we examined the spatial relationships using a biplot of component scores.

Results

Larval Walleye Abundance and Distribution

Pelagic walleye larvae were most abundant in 1994 when densities peaked at over 92.5 walleye /1,000 m^3. Larval walleye abundance was low in 1995 and 1999 when the peak density reached only 5.2 and 4.3 fish/1,000 m^3 respectively. Larval abundance was moderate in 1996, 1997, and 1998 with peak densities of 42.3, 30.9, and 16.8 pelagic larval walleye/1,000 m3 of water sampled (Figures 2 and 3). Walleye densities were consistently higher at shallow nearshore areas of the study area than at deep offshore sites in all years of the study (Figures 4 and 5). Walleye density was inversely correlated with depth and while this relationship was weak, it was significant (Table 1; Figure 6). Densities of pelagic walleye larvae were higher at western sites in 1996, 1998, and 1999 while fish were more evenly distributed in 1994, 1995, and 1997 (Figures 4 and 5).

Ichthyoplankton Abundance and Distribution

Ichthyoplankton prey densities generally showed an increasing trend in abundance throughout June of most years. Ichthyoplankton prey were most abundant in June of 1998 with the mean abundance increasing from about 1,000 fish/1,000 m^3 of water sampled in early June to over 2,000 fish/ 1,000 m^3 at the end of the month. Ichthyoplankton were least abundant in 1995 when the mean density in June never exceeded 500 fish/1,000 m^3 of water sampled. Ichthyoplankton density was quite high in early June of 1994 but decreased to less than 500 fish/1,000 m^3 during mid-June before increasing to over 2,500/1,000 m^3 at the end of June. Ichthyoplankton densities in 1996, 1997, and 1999 were quite similar increasing steadily throughout June to a peak just above 500 fish/1,000 m^3 (Figure 7).

Distribution of ichthyoplankton was generally higher at shallow nearshore sites (Figures 8 and 9), although there was considerably more variation in ichthyoplankton distributions than walleye distributions (Figures 4 and 5). We found a significant but weak negative correlation between depth and ichthyoplankton abundance (Table 1; Figure 6). Densities of ichthyoplankton were noticeably higher at western sites in 1996 and 1999 and noticeably lower in western sites in 1995. Ichthyoplankton were more evenly distributed in 1994, 1997, and 1998 (Figures 8 and 9).

Zooplankton Abundance and Distribution

Zooplankton numbered about 10 per liter in late April and early May 1996, and 1998 and increased at a similar rate in both years to just over 40 individuals per liter by

June 15. Zooplankton were most abundant in the spring of 1999 with an initial density of about 10 individuals per liter but a large increase in late May to over 130 per liter by June 15. Zooplankton were least abundant in 1997, not exceeding 20 organisms per liter during May and early June (Figure 10). Zooplankton were generally more abundant at inshore sites in 1996 and 1999 but this trend was not as evident in 1997 and 1998 (Figures 11 and 12). We found a weak but significant negative correlation between depth and zooplankton abundance across all years sampled (Table 1; Figure 6).

Physical Habitat Attributes

Water temperatures were generally warmer at inshore sites than at offshore sites in all years when water temperatures were recorded. Water temperatures consistently exceeded the daily mean water temperature at shallow nearshore sites (Figure 13 and 14). Water temperature was significantly negatively correlated with depth although the relationship was weak (Table 1; Figure 6). Secchi disk readings varied widely between sampling sites and sampling dates but were generally lower (darker water) at nearshore sites than at offshore sites in all years (Figures 15 and 16). Secchi disk depth was significantly positively correlated with depth, although this relationship was weak (Table 1; Figure 6). Nearshore bottom substrate characteristics in our study area, as reported in Fuller (1996), were dominated by a 300 m wide sand beach/bar complex. In many areas along the coast, a 200 to 800 m wide strip of till and till related deposits lie lakeward of the sand beach/bar complex. Muddy sand makes up the majority of the bottom lakeward of the till extending out to about 3.2 km from shore which was the extent of the mapped area reported in Fuller (1996).

Principal Components Analysis

We selected the first two principal components for graphical analysis. Principal component 1 had an eigenvalue of 2.99 and explained over 59% of the variability in the dataset while principal component 2 had an eigenvalue of 0.99 and explained an additional 19.8% of the variability. These two principal components represented the sharp descending left limb of the scree diagram (Figure 17). The biplot of the principal component scores revealed a good separation of sample sites by depth. The graphical analysis shows that principal component 1 separates shallow nearshore sites and deeper offshore sites while principal component 2 provides a tight cluster of the deepest sites (Figure 17) indicating that these principal components represent gradations in larval walleye density and associated physical and biological habitat attributes based on site depth and distance from shore (Table 2).

Discussion

Our study demonstrates repeatable patterns in pelagic larval walleye distribution. We found larval walleye to become concentrated in shallow nearshore areas in all six years of our study. These areas generally had warmer and darker waters than offshore sites and also had more abundant zooplankton and ichthyoplankton prey resources. These physical and biological habitat conditions are favorable as nursery habitat for larval walleye and promote good growth and survival. For example, growth rate and development of walleye sac-fry is temperature dependent as temperature determines the rate of yolk absorption while growth of post sac-fry is a function of food consumption and metabolism, both of which are temperature regulated (McElman and Balon 1979, Johnston and Mathias 1994). Studies have shown that walleye larvae have higher gas bladder inflation rates, higher prey consumption and assimilation rates, faster swimming speeds, faster growth rates, and higher survival rates in warmer waters than in cold waters (Clapp et al. 1997, Regier and Summerfelt 1999, Trometer and Busch 1999). Faster growth of age-0 walleye moves fish through the size-specific predatory gauntlet faster, thereby reducing the potential for predation and other mortality agents that can occur during vulnerable early life history stages.

Productivity of prey resources is also generally higher in warmer waters than cooler waters (Wetzel 1975) providing fish with an additional growth advantage by inhabiting areas with warmer waters. Our data indicate that zooplankton densities were generally higher at nearshore sites during late April and May when walleye are zooplanktivorous (Roseman 1997). Ichthyoplankton prey were also generally more abundant in nearshore areas in June when age-0 walleye switch from eating zooplankton to fish (Roseman 1997). The literature abounds with evidence corroborating the positive relationship between prey abundance and larval walleye growth and survival (Carlander and Payne 1977, Kelso 1972, Kempinger and Churchill 1972, Mills and Forney 1988, Fox 1989, Roseman 1997).

Nearshore waters were also generally more turbid than offshore waters in all years of our study. Laboratory studies have shown that larval walleye had faster swimming speeds, faster growth, improved gas bladder inflation, and higher survival rates in darker waters (Bristow et al. 1996, Regier and Summerfelt 1997). In western Lake Erie, nearshore waters are darker due to the mixing action of lake waters against the shoreline and the input of suspended sediments from tributaries (Burns 1985). Darker water could have increased the efficiency of our sampling gear (Hanson and Rudstam 1995) accounting in part for the higher densities of pelagic walleye larvae we observed in nearshore waters. However, pelagic walleye larvae are positively phototropic (McElman and Balon 1979) and are not good swimmers (Houde 1969) so avoidance of our sampling gear in clearer offshore waters was likely minimal.

We were able to demonstrate the repeatable relationship between pelagic larval walleye and the physical and biological habitat components using both spatial and statistical models. The GIS analysis results clearly demonstrated that walleye larvae became concentrated at nearshore sites in all six years of our study. The GIS analysis also revealed repeatable patterns in habitat attributes and how walleye larvae overlapped in time and space with habitat conditions conducive to good walleye growth and survival (warmer and darker waters, higher prey densities). Our statistical analysis supported the results of the spatial analysis by corroborating the relationships defined in the GIS output. Principal components analysis further emphasizes the relationship between site location and attribute value by demonstrating gradations in larval walleye density and associated physical and biological habitat attributes based on site depth and distance from shore. Correlation analysis revealed significant relationships between site depth and attribute values further emphasizing nearshore/offshore gradients. Even though our correlation coefficients revealed weak relationships between variables, these results were highly significant and based on large sample sizes (Table 1).

Ultimately, our research underscores the importance of western Lake Erie coastal areas as walleye nursery areas and emphasizes the need to understand coastal processes and their effects on fish habitat for several reasons. First, water in western Lake Erie has a short residence time of only about 2.5 months (Burns 1985). This implies that habitat conditions have the potential for rapid change in these areas. Second, water currents act as the link between important reef spawning areas and the nearshore nursery areas. Lake hydrology determines the direction and speed in which larvae will be transported and drives the degree of spatial and temporal overlap of larvae with physical and biological habitat components. These currents provide the physical linkage between egg incubation areas and the warmer, more productive coastal zone nursery areas. The lack of information on water current patterns and their role in larval walleye dispersal and distribution represents a void in our knowledge about walleye ecology in western Lake Erie. Thirdly, hydrology facilitates the overlap of larval walleye with patchy habitat resources. Our results showed that larval walleye life history requirements are best met in these nearshore coastal areas where waters were warmer, darker, and prey resources were generally greater than offshore areas. Lastly, the effects of human impact within the narrow coastal community is usually greatest and, because of the limited area of such communities, the chances for large-scale deleterious effects are enhanced.

Our research identified that nearshore coastal areas in western Lake Erie are important as nursery habitat for fish and emphasizes the need to restore and protect these areas. In the last half of the 20th century the quantity of this habitat was greatly reduced and the natural coastal processes (currents, sediment movements, thermal regime; Bowden 1983) were modified. Much of the shoreline in western Lake Erie has been reinforced with hard materials to prevent erosion and act as flood control. This armoring of the shoreline removes the natural land/water interface and interferes with lacustrine processes responsible for structuring the limnological characteristics of nearshore waters important as nursery habitat for walleye and other fishes. Coastal zone planners should consider the biological value of these coastal areas and their associated natural processes. Efforts should be devoted to reconstructing natural hydrologic patterns to facilitate the continued restoration of Lake Erie and its fisheries.

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Table 1. Correlations between sample site depth (m) and deviation from mean water temperature (C), deviation from mean secchi disk reading (m), deviation from mean zooplankton density (#/l), deviation from mean ichthyoplankton density (#/1,000 m^3), deviation from mean walleye density (#/1,000 m^3), and between the deviations of the mean of secchi disk depth and walleye density. N indicates sample size, r indicates correlation coefficient, and p indicates level of significance.

Correlation	N	r	p
Depth X Temperature	116	-0.771	<0.001
Depth X Secchi	718	0.238	<0.001
Depth X Zooplankton Density	718	-0.209	0.044
Depth X Ichthyoplankton Density	718	-0.144	<0.001
Depth X Walleye Density	718	-0.201	<0.001
Secchi X Walleye Density	718	-0.170	<0.001

Table 2. Factor loadings for first two principal components used in graphical analysis.

Variable	Principle Component 1	Principle Component 2
Walleye abundance	0.507694	-0.25494
Ichthyoplankton abundance	0.484708	-0.84509
Zooplankton abundance	0.235390	0.896916
Temperature	0.497391	0.074385
Secchi depth	-0.45221	0.426265

List of Figures.

Figure 1. Map of western Lake Erie study area. Filled circles identify sample sites. Contour interval is 2 m.

Figure 2. Log-transformed (Ln Catch +1 #/1,000 m^3) densities of pelagic walleye larvae collected from sites in western Lake Erie, 1994 –1996.

Figure 3. Log-transformed (Ln Catch +1 #/1,000 m^3) densities of pelagic walleye larvae collected from sites in western Lake Erie, 1997-1999.

Figure 4. Deviations from the annual mean value for pelagic larval walleye density at sampling sites in western Lake Erie in spring, 1994-1996.

Figure 5. Deviations from the annual mean value for pelagic larval walleye density at sampling sites in western Lake Erie in spring, 1994-1996.

Figure 6. Relationship between depth and water temperature (panel A), depth and secchi disk depth (panel B), depth and zooplankton density (panel C), depth and ichthyoplankton density (panel D), depth and pelagic larval walleye density (panel E), and secchi disk depth and walleye density (panel F) at sample sites in western Lake Erie from 1994 – 1999.

Figure 7. Abundance of ichthyoplankton prey at nearshore sites in western Lake Erie during the period 10 June – 30 June, 1994 – 1999.

Figure 8. Deviations from mean annual values for non-walleye ichthyoplankton prey species at sampling sites in western Lake Erie in spring, 1994-1996.

Figure 9. Deviations from mean annual values for non-walleye ichthyoplankton prey species at sampling sites in western Lake Erie in spring, 1997-1999.

Figure 10. Abundance of zooplankton at nearshore sites in western Lake Erie during the period from May 1 – June 10,

Figure 11. Deviations from mean annual values for zooplankton at sampling sites in western Lake Erie in spring, 1996 and 1997.

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Figure 13. Deviations from mean annual values for water temperature at sampling sites in western Lake Erie in spring, 1996 and 1997.

Figure 14. Deviations from mean annual values for water temperature at sampling sites in western Lake Erie in spring, 1998 and 1999.

Figure 15. Deviations from mean annual values for secchi disk depth at sampling sites in western Lake Erie in spring, 1994, 1995, and 1996.

Figure 16. Deviations from mean annual values for secchi disk depth at sampling sites in western Lake Erie in spring, 1997, 1998, and 1999.

Figure 17. Top graph is a scree diagram indicating eigenvalues and proportion of variation explained by individual principal components. Bottom graph is a biplot of principal components 1 and 2 demonstrating the separation of sample sites by depth.

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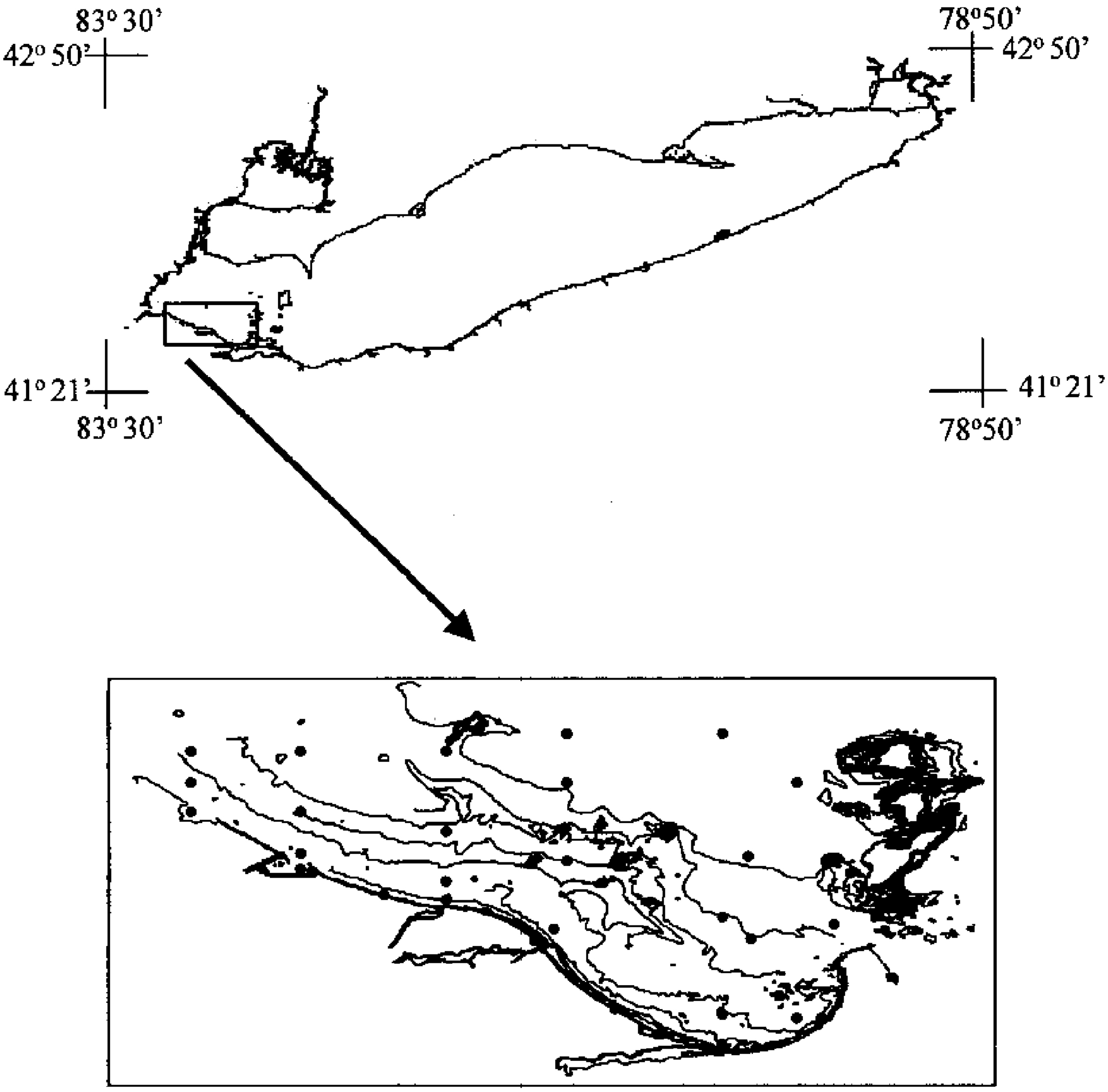


Fig 1

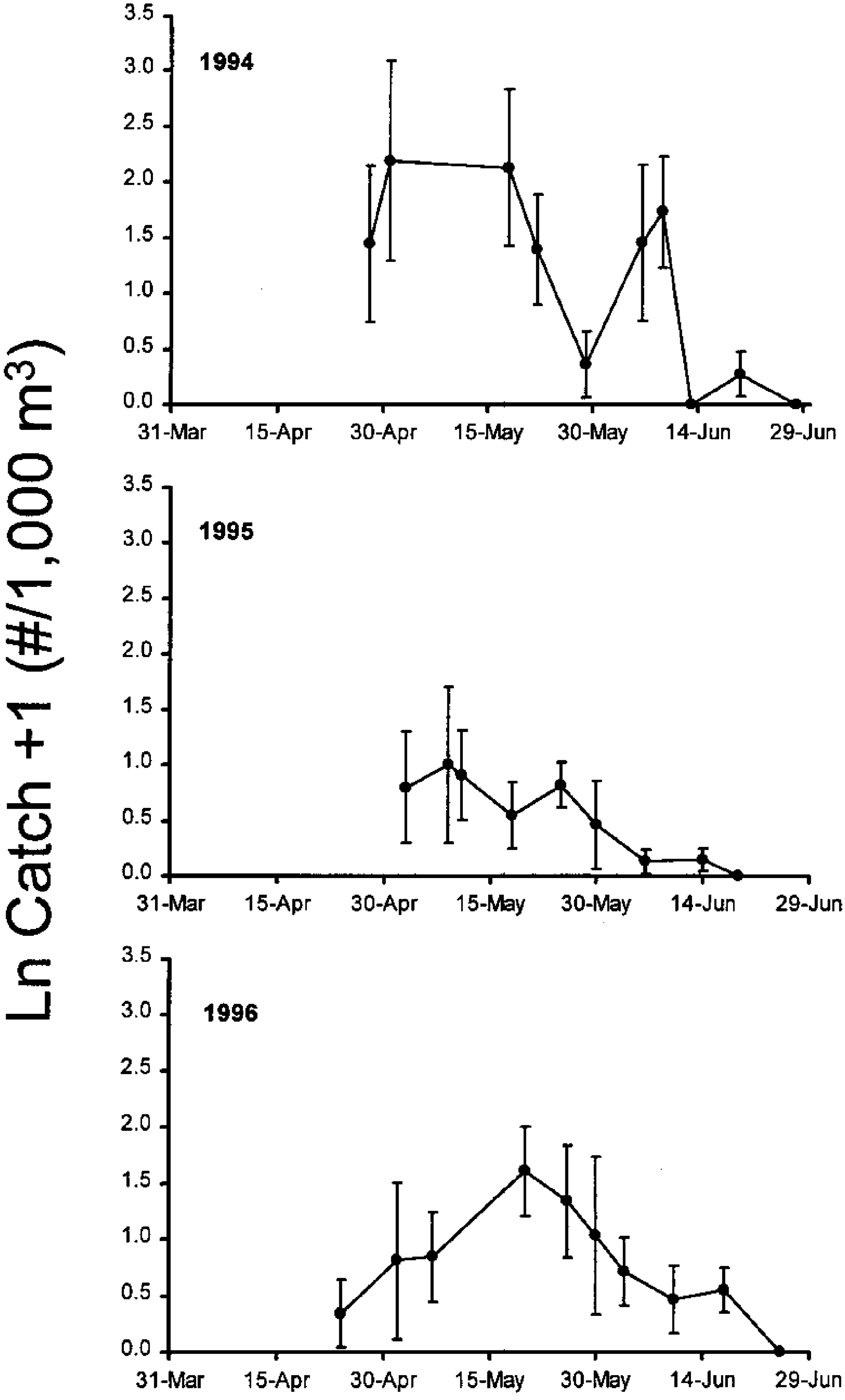

Ln Catch +1 (#/1,000 m^3)
1994
1995
1996
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
31-Mar
15-Apr
30-Apr
15-May
30-May
14-Jun
29-Jun

Fig 2

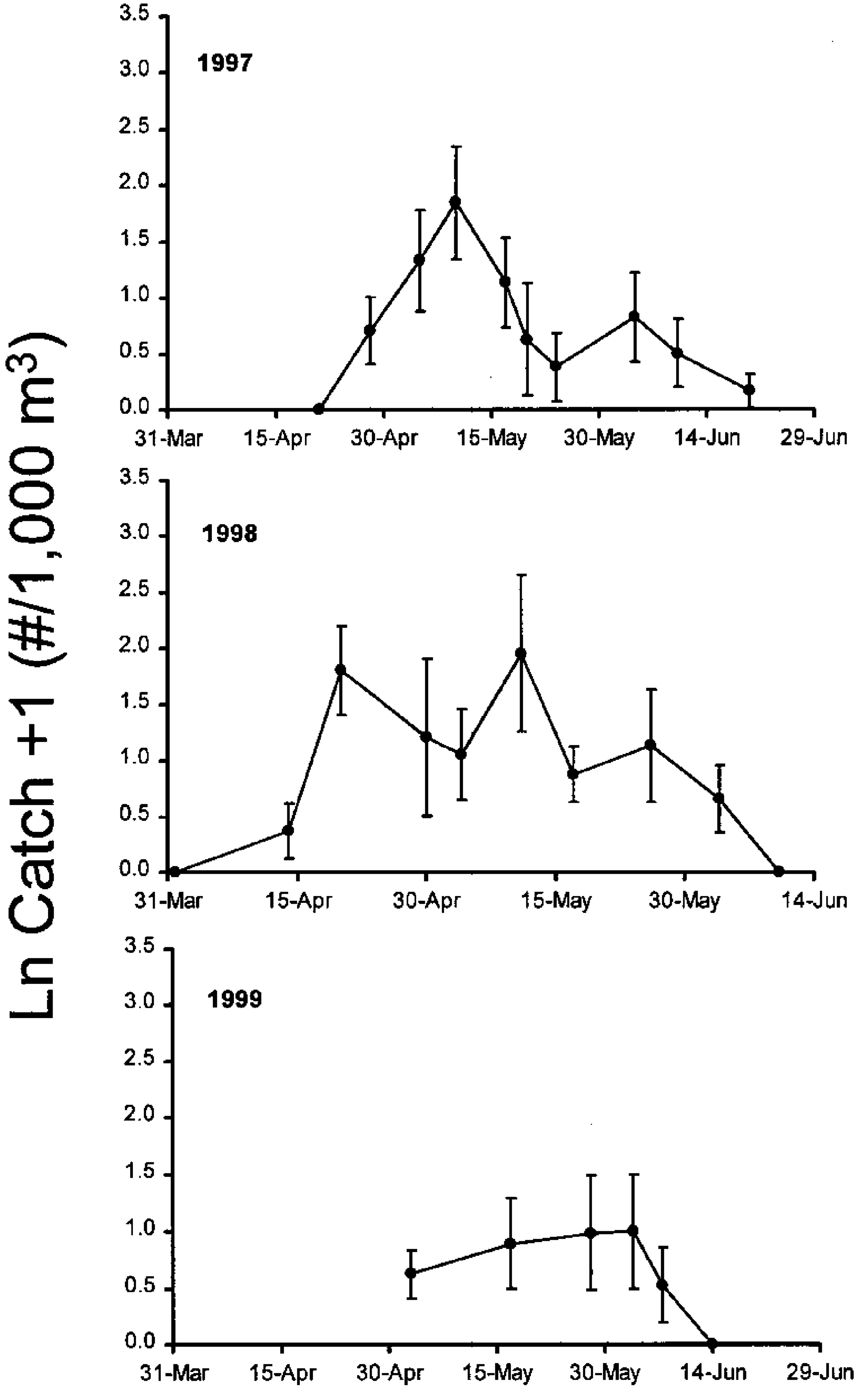

Ln Catch +1 (#/1,000 m^3)
1997
1998
1999
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
31-Mar
15-Apr
30-Apr
15-May
30-May
14-Jun
29-Jun

Fig 3

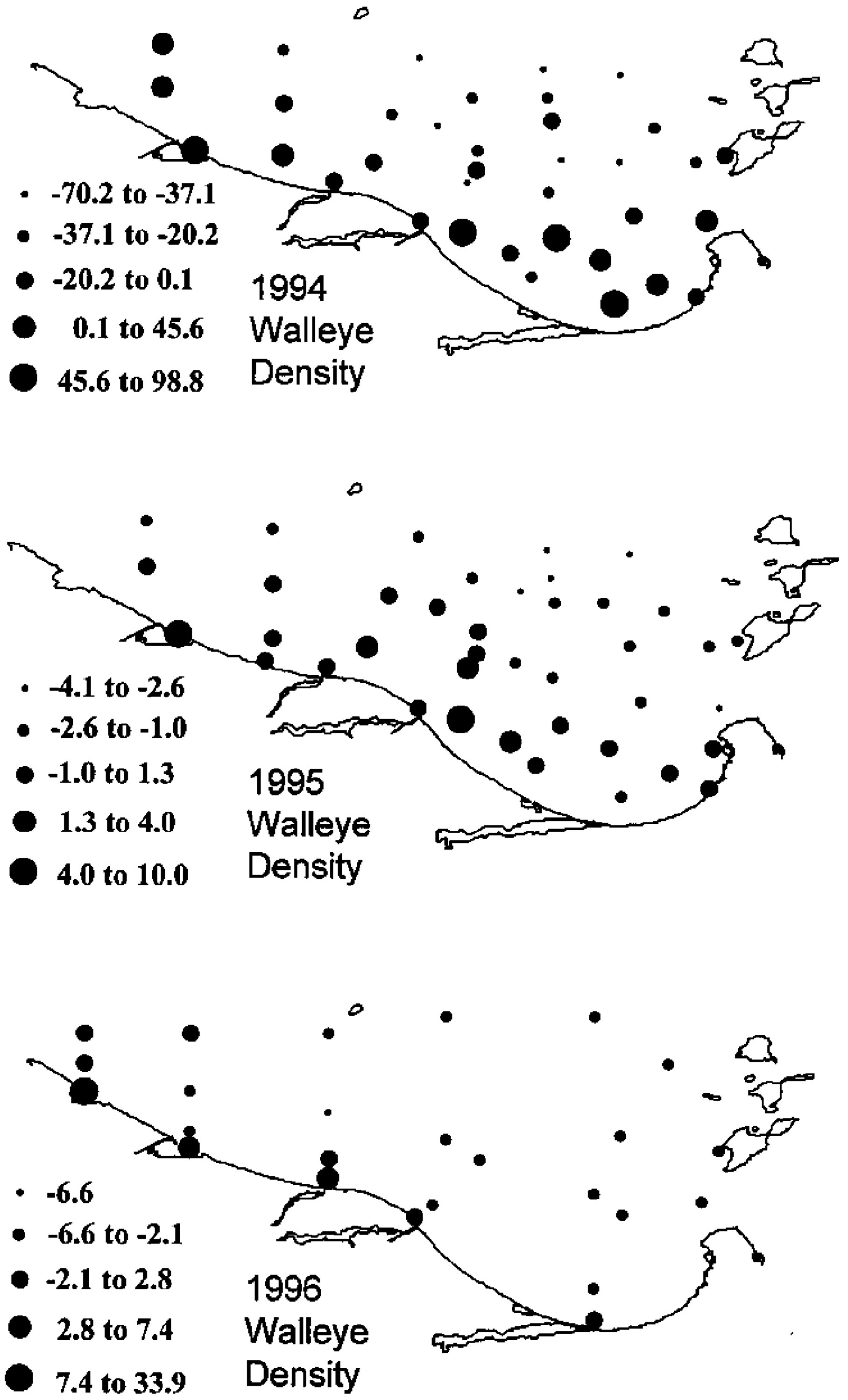
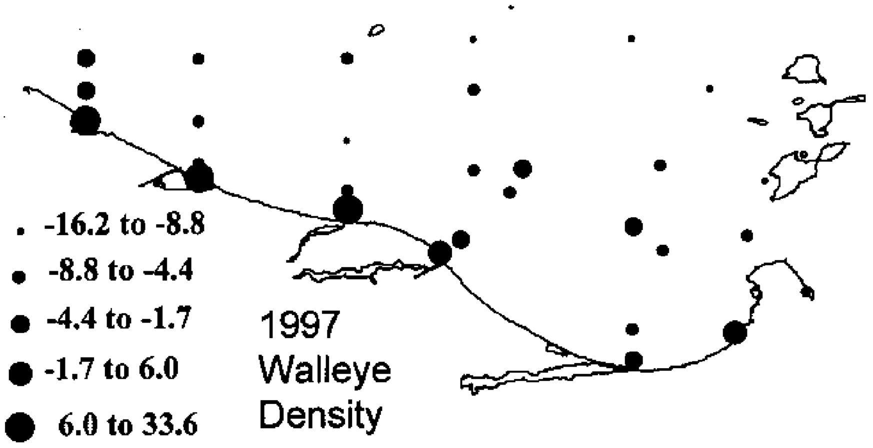
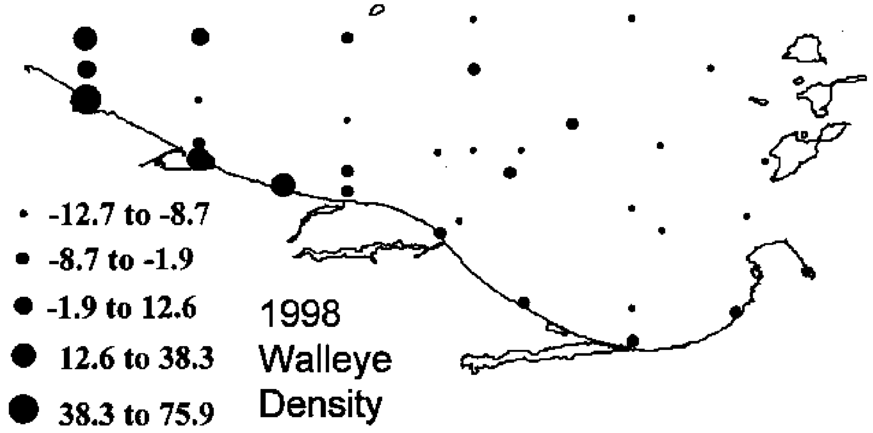

-70.2 to -37.1
-37.1 to -20.2
-20.2 to 0.1
0.1 to 45.6
45.6 to 98.8
1994
Walleye
Density
-4.1 to -2.6
-2.6 to -1.0
-1.0 to 1.3
1.3 to 4.0
4.0 to 10.0
1995
Walleye
Density
-6.6
-6.6 to -2.1
-2.1 to 2.8
2.8 to 7.4
7.4 to 33.9
1996
Walleye
Density

Fig 4


1997 Walleye Density


1998 Walleye Density

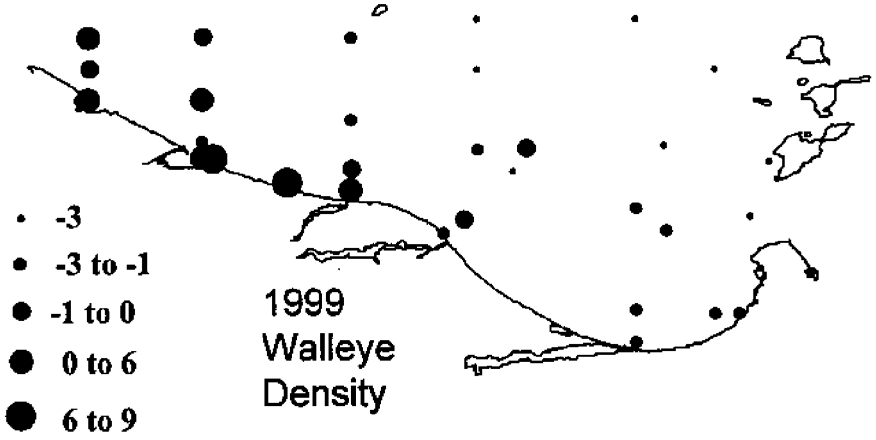

1999 Walleye Density

Fig 5

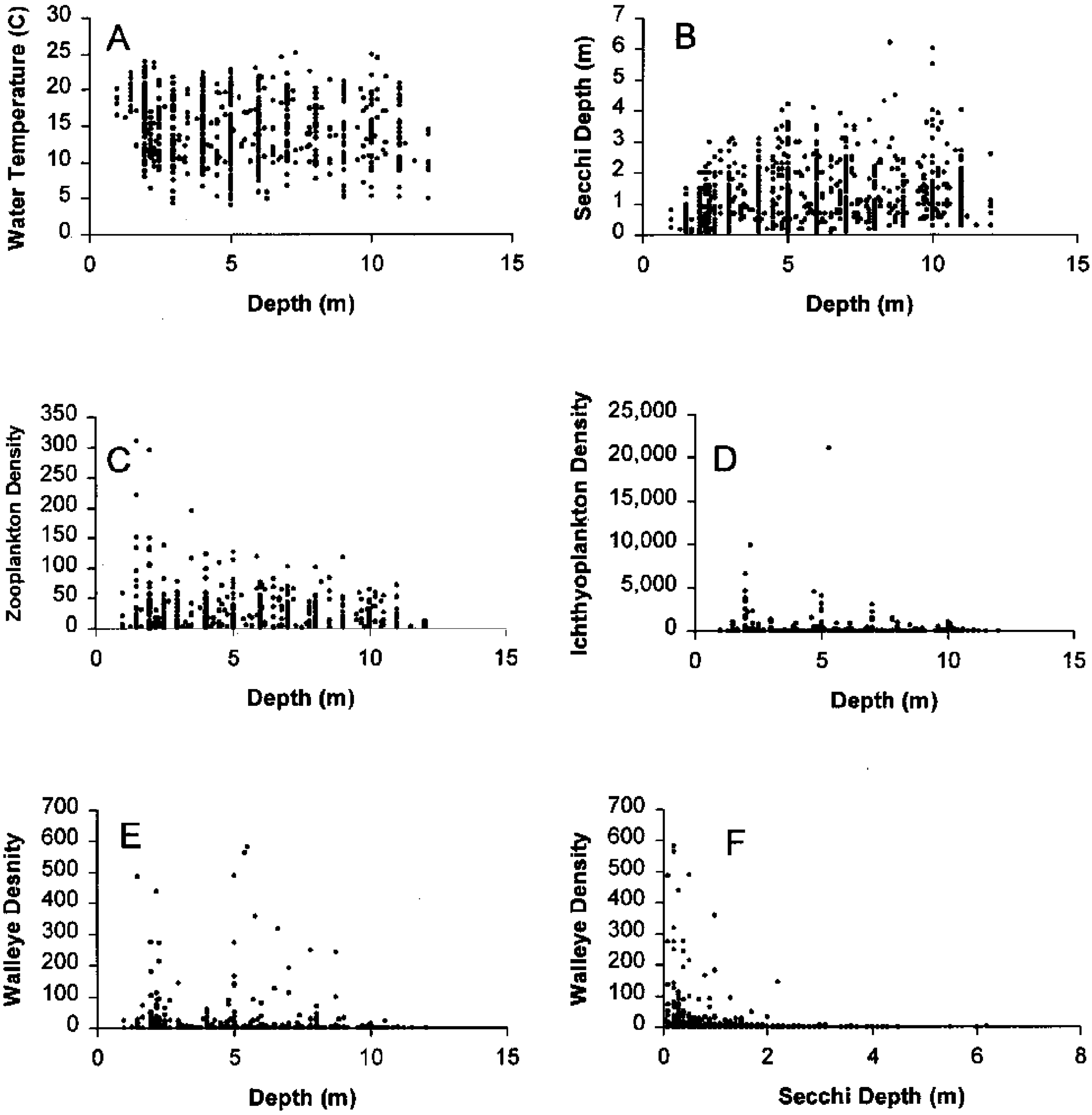

A
Water Temperature (C)
30
25
20
15
10
5
0
Depth (m)
0
5
10
15
B
Secchi Depth (m)
7
6
5
4
3
2
1
0
Depth (m)
0
5
10
15
C
Zooplankton Density
350
300
250
200
150
100
50
0
Depth (m)
0
5
10
15
D
Ichthyoplankton Density
25,000
20,000
15,000
10,000
5,000
0
Depth (m)
0
5
10
15
E
Walleye Desnity
700
600
500
400
300
200
100
0
Depth (m)
0
5
10
15
F
Walleye Density
700
600
500
400
300
200
100
0
Secchi Depth (m)
0
2
4
6
8

Fig 6

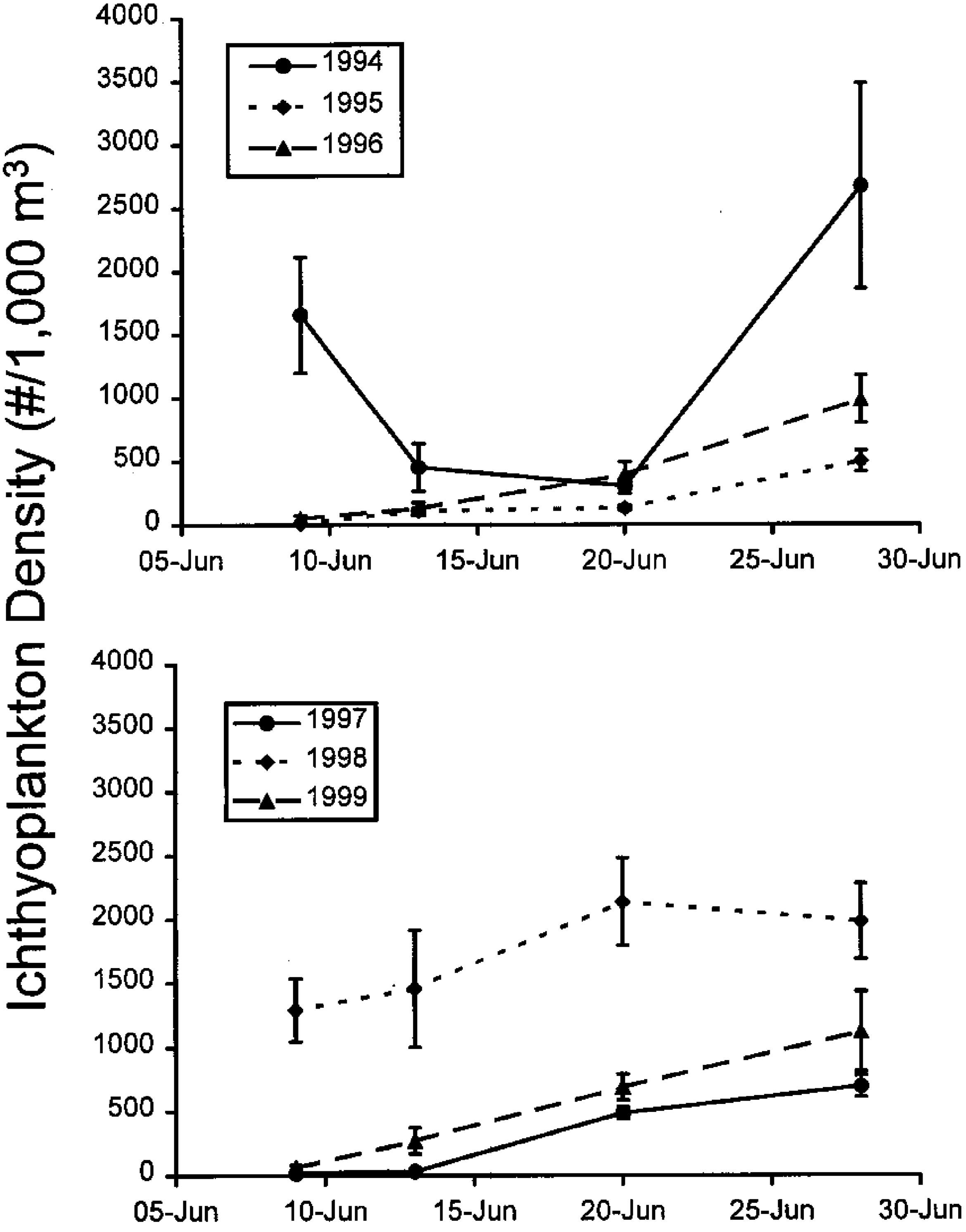

Ichthyoplankton Density (#/1,000 m³)
4000
3500
3000
2500
2000
1500
1000
500
0
1994
1995
1996
05-Jun
10-Jun
15-Jun
20-Jun
25-Jun
30-Jun
4000
3500
3000
2500
2000
1500
1000
500
0
1997
1998
1999
05-Jun
10-Jun
15-Jun
20-Jun
25-Jun
30-Jun

Fig 7

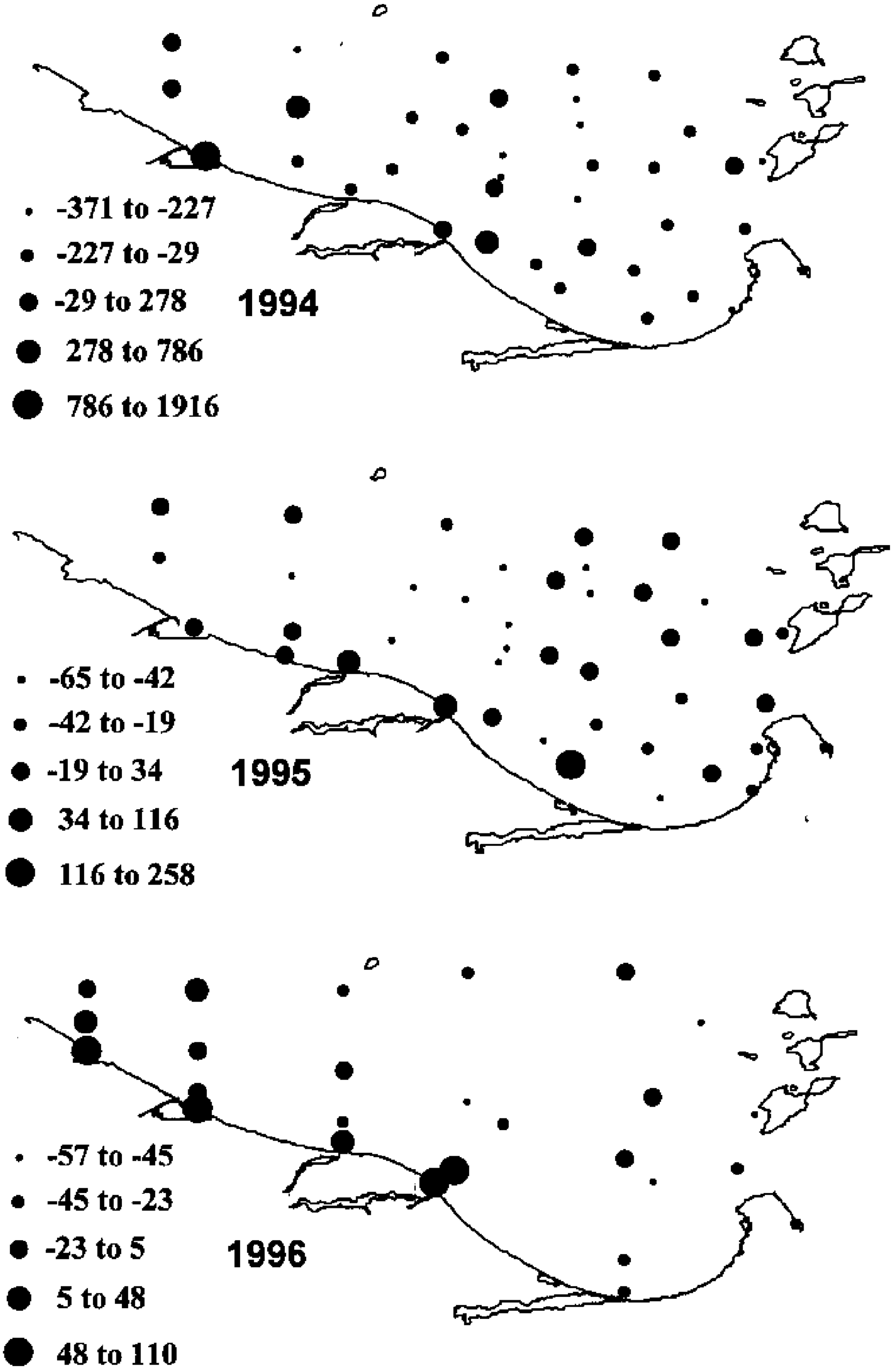

-371 to -227
-227 to -29
-29 to 278
278 to 786
786 to 1916
1994
-65 to -42
-42 to -19
-19 to 34
34 to 116
116 to 258
1995
-57 to -45
-45 to -23
-23 to 5
5 to 48
48 to 110
1996

Fig 8

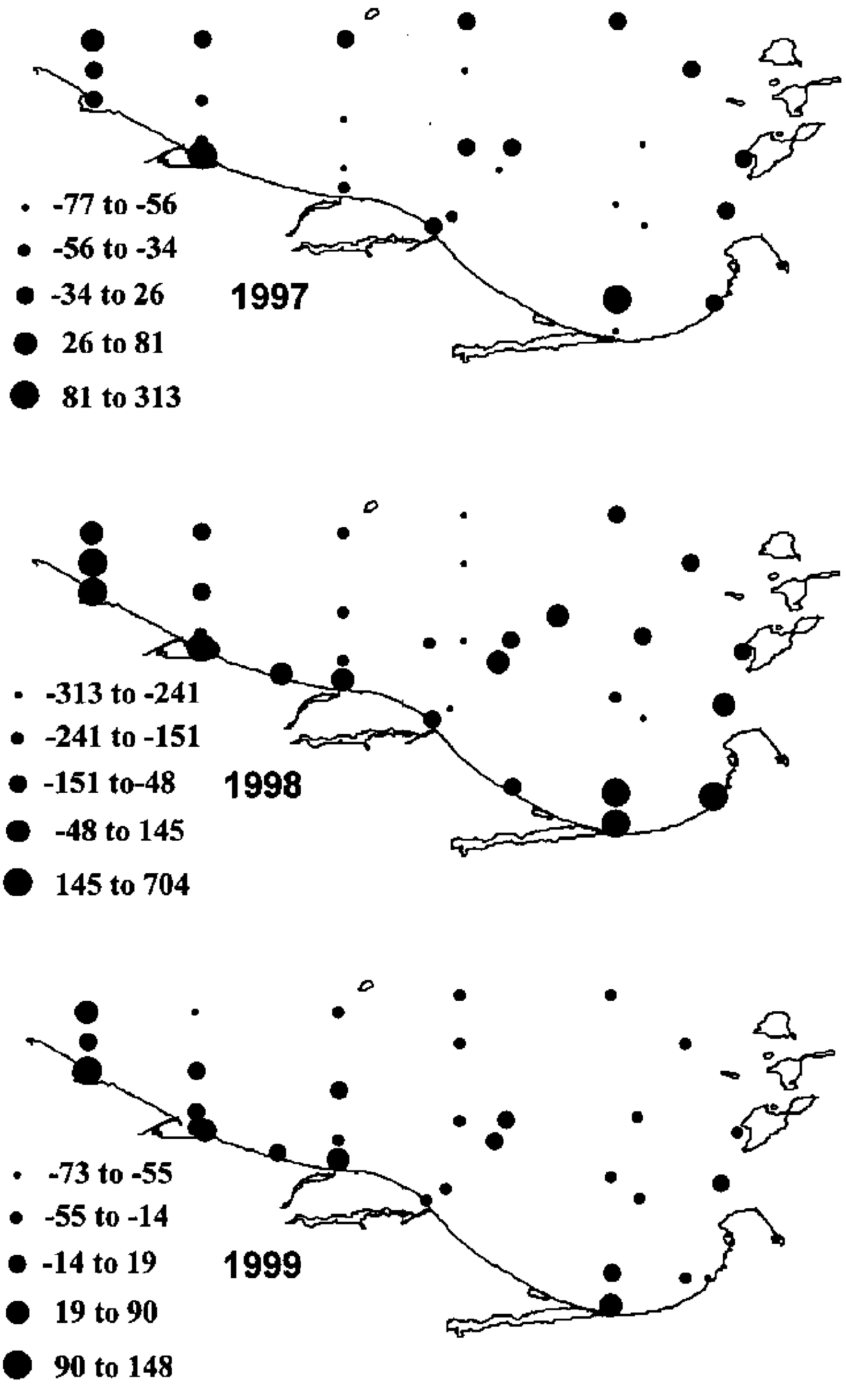

-77 to -56
-56 to -34
-34 to 26
26 to 81
81 to 313
1997
-313 to -241
-241 to -151
-151 to-48
-48 to 145
145 to 704
1998
-73 to -55
-55 to -14
-14 to 19
19 to 90
90 to 148
1999

Fig 9

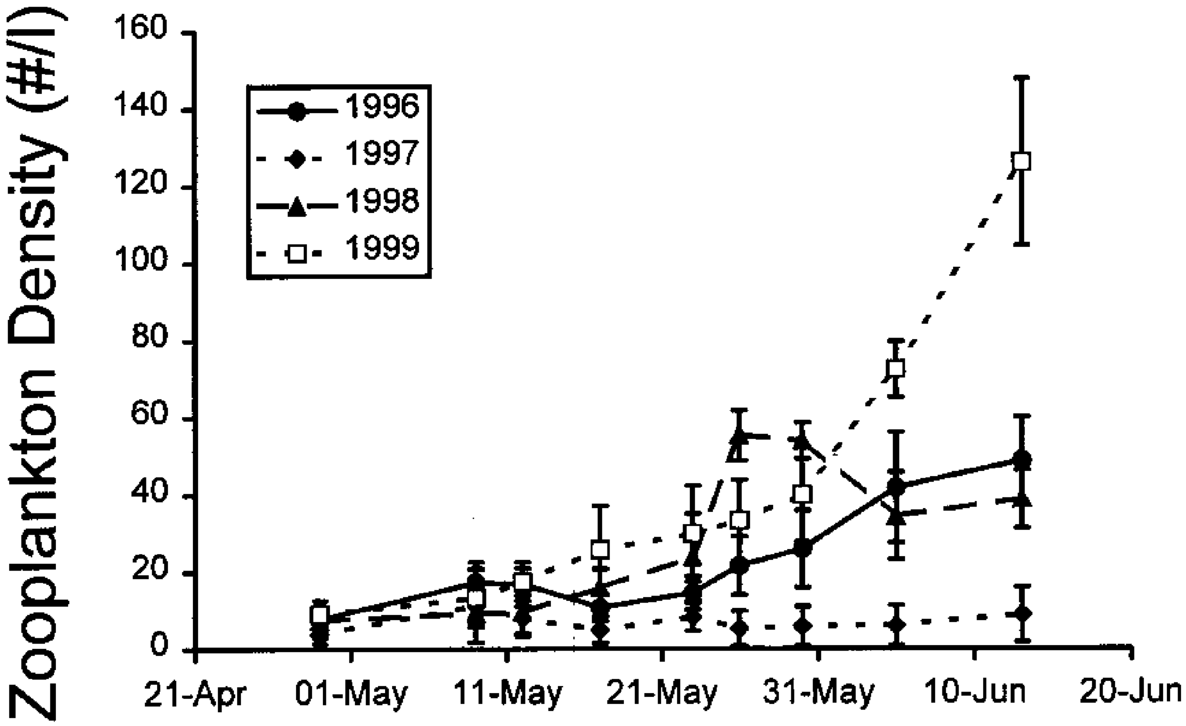
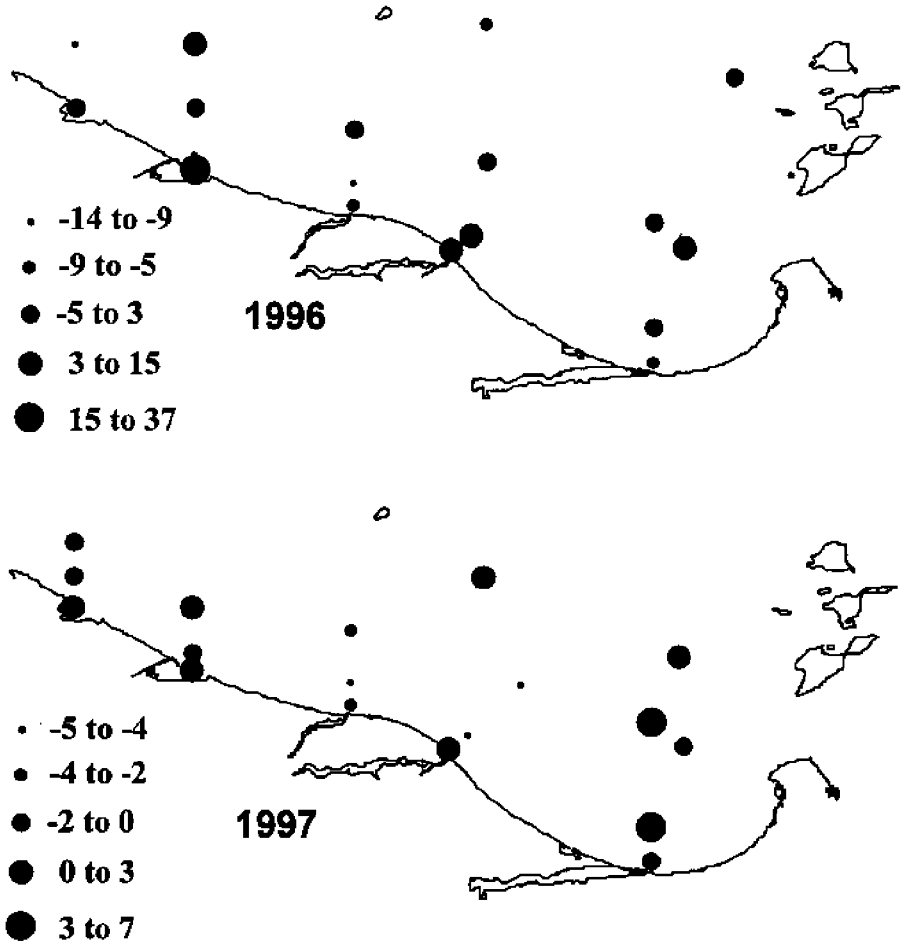

Zooplankton Density (#/l)
160
140
120
100
80
60
40
20
0
21-Apr
01-May
11-May
21-May
31-May
10-Jun
20-Jun
1996
1997
1998
1999

Fig 10



-14 to -9
-9 to -5
-5 to 3
3 to 15
15 to 37
1996
-5 to -4
-4 to -2
-2 to 0
0 to 3
3 to 7
1997

Fig 11

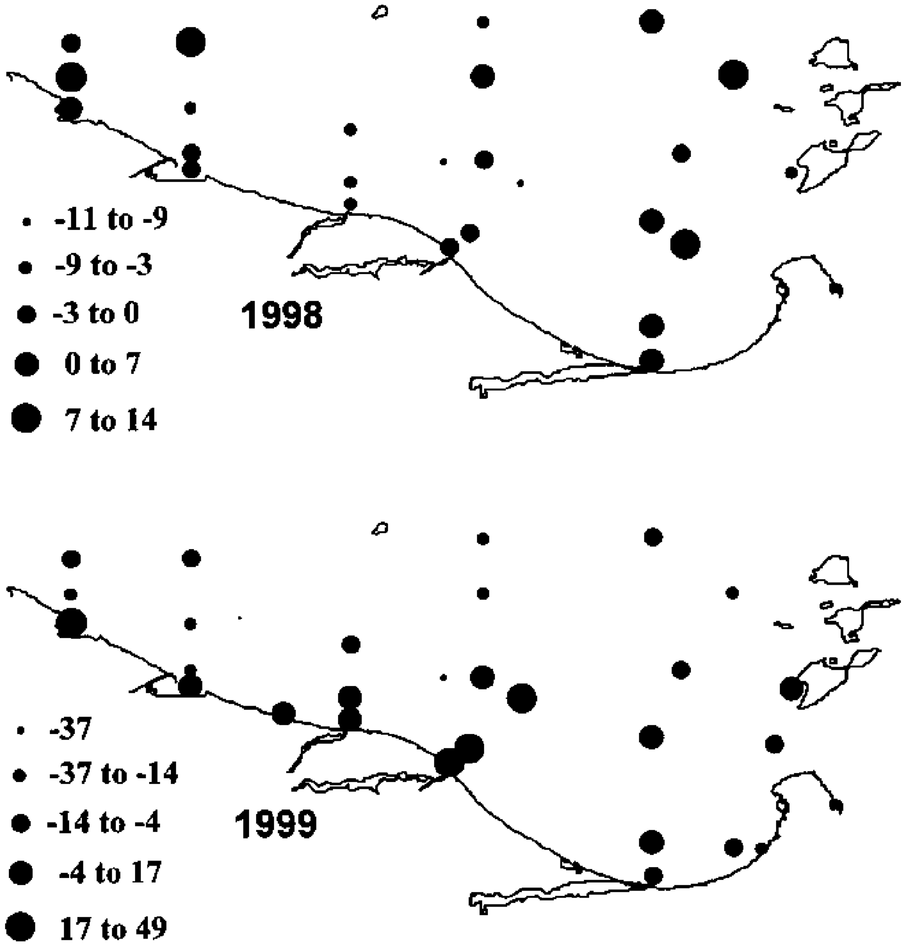
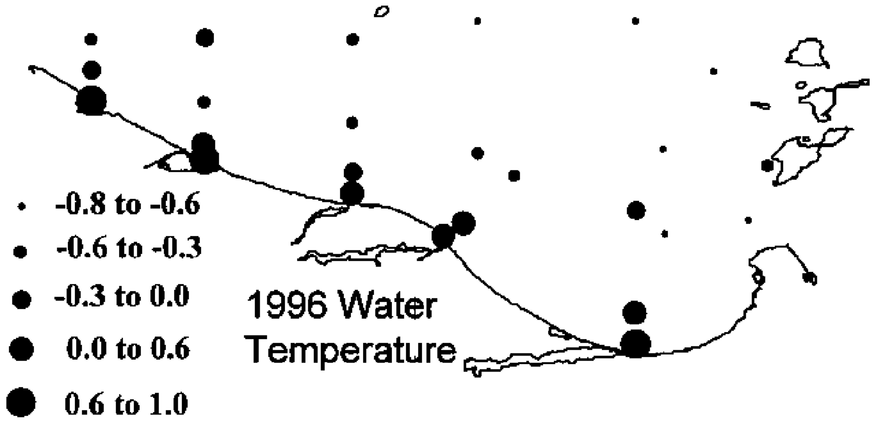

-11 to -9
-9 to -3
-3 to 0
0 to 7
7 to 14
1998
-37
-37 to -14
-14 to -4
-4 to 17
17 to 49
1999

Fig 12


-0.8 to -0.6
-0.6 to -0.3
-0.3 to 0.0
0.0 to 0.6
0.6 to 1.0
1996 Water Temperature

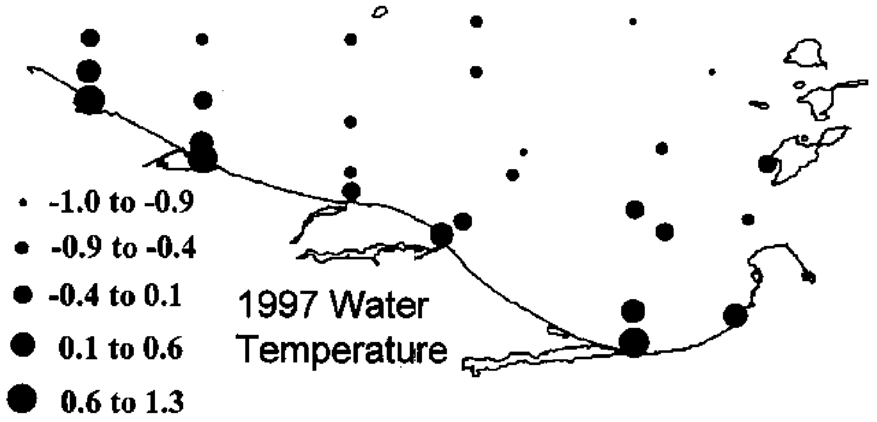

-1.0 to -0.9
-0.9 to -0.4
-0.4 to 0.1
0.1 to 0.6
0.6 to 1.3
1997 Water Temperature

Fig 13

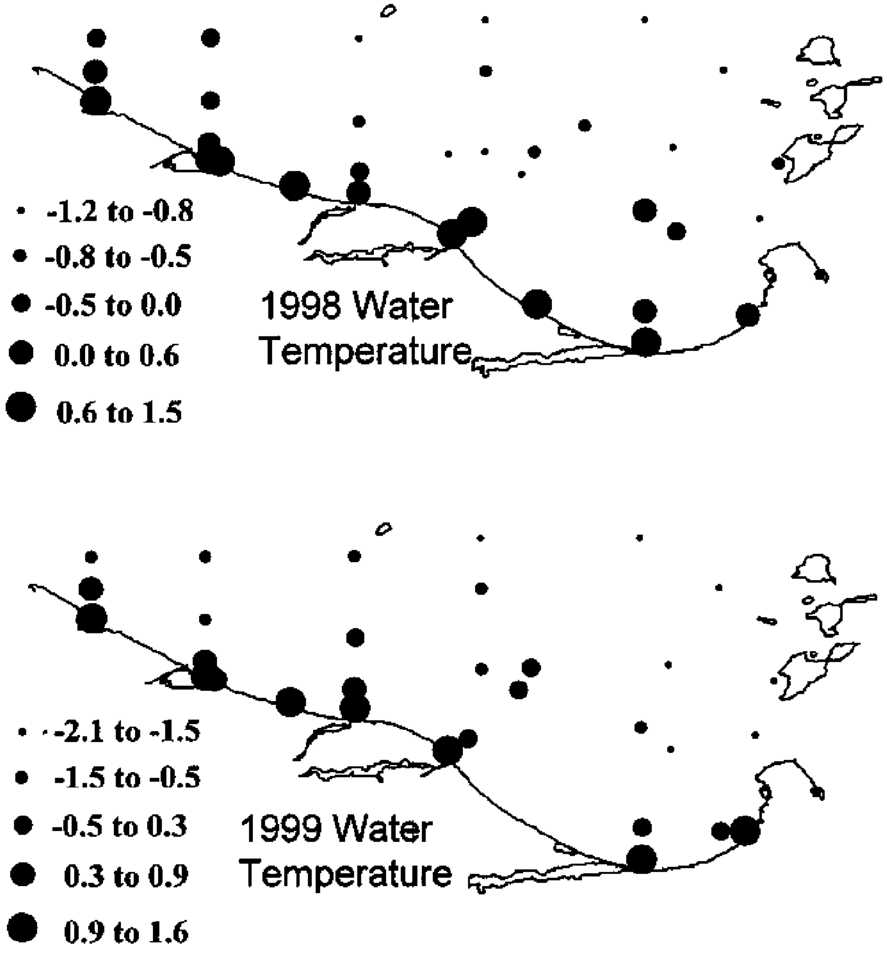

-1.2 to -0.8
-0.8 to -0.5
-0.5 to 0.0
0.0 to 0.6
0.6 to 1.5
1998 Water Temperature
-2.1 to -1.5
-1.5 to -0.5
-0.5 to 0.3
0.3 to 0.9
0.9 to 1.6
1999 Water Temperature

Fig 14

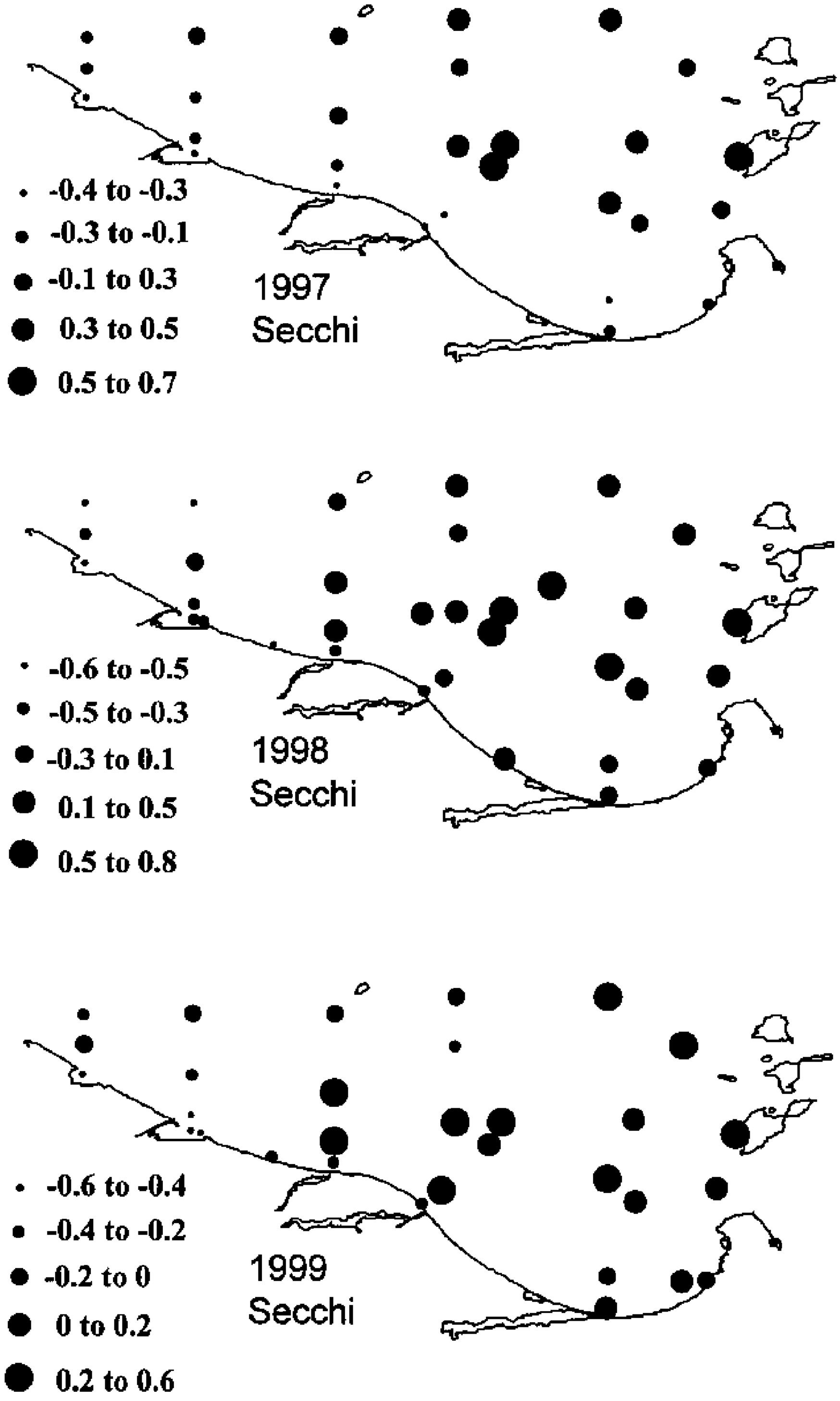

-0.4 to -0.3
-0.3 to -0.1
-0.1 to 0.3
0.3 to 0.5
0.5 to 0.7
1997
Secchi
-0.6 to -0.5
-0.5 to -0.3
-0.3 to 0.1
0.1 to 0.5
0.5 to 0.8
1998
Secchi
-0.6 to -0.4
-0.4 to -0.2
-0.2 to 0
0 to 0.2
0.2 to 0.6
1999
Secchi

Fig 15

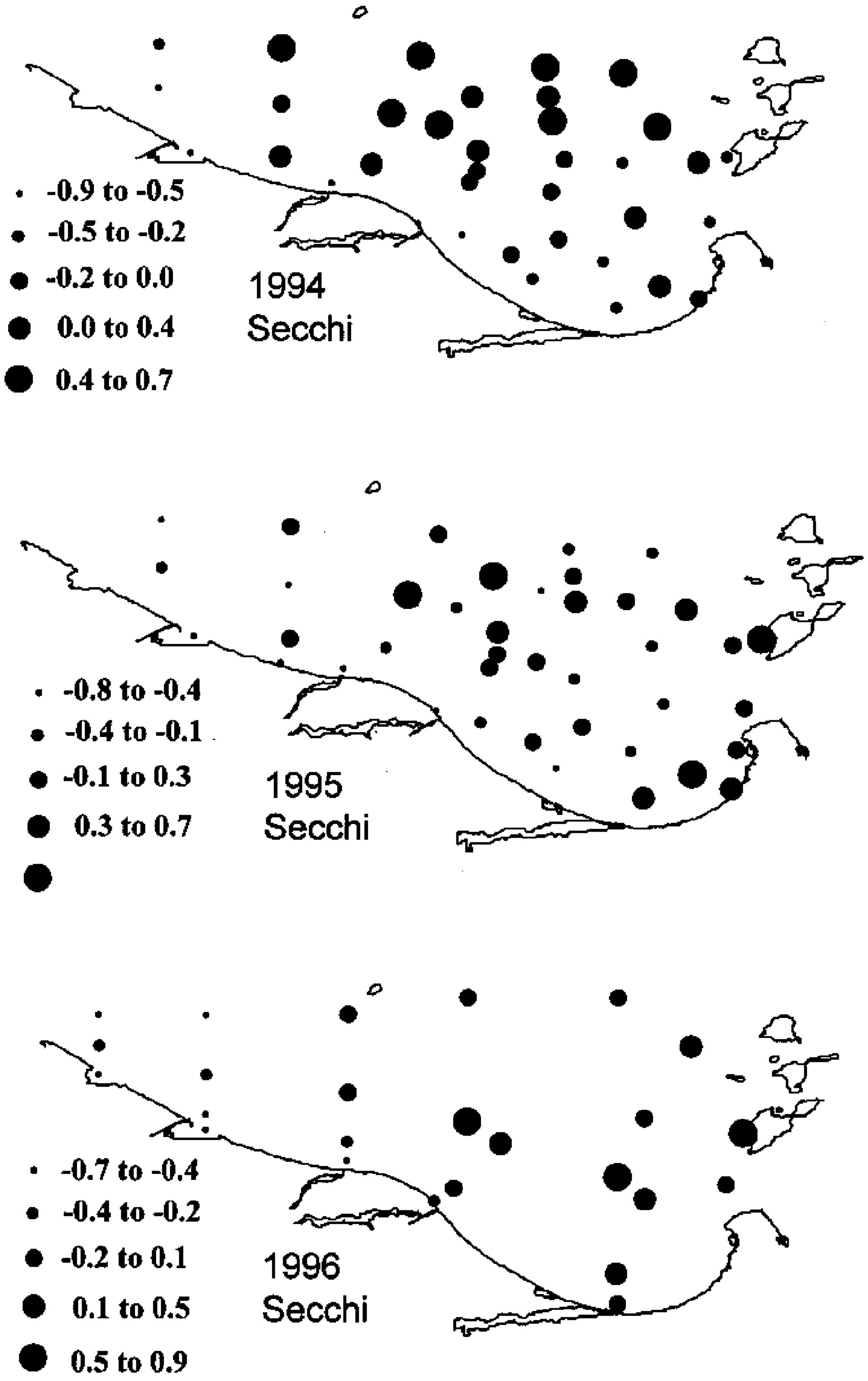

-0.9 to -0.5
-0.5 to -0.2
-0.2 to 0.0
0.0 to 0.4
0.4 to 0.7
1994
Secchi
-0.8 to -0.4
-0.4 to -0.1
-0.1 to 0.3
0.3 to 0.7
1995
Secchi
-0.7 to -0.4
-0.4 to -0.2
-0.2 to 0.1
0.1 to 0.5
0.5 to 0.9
1996
Secchi

Fig 16

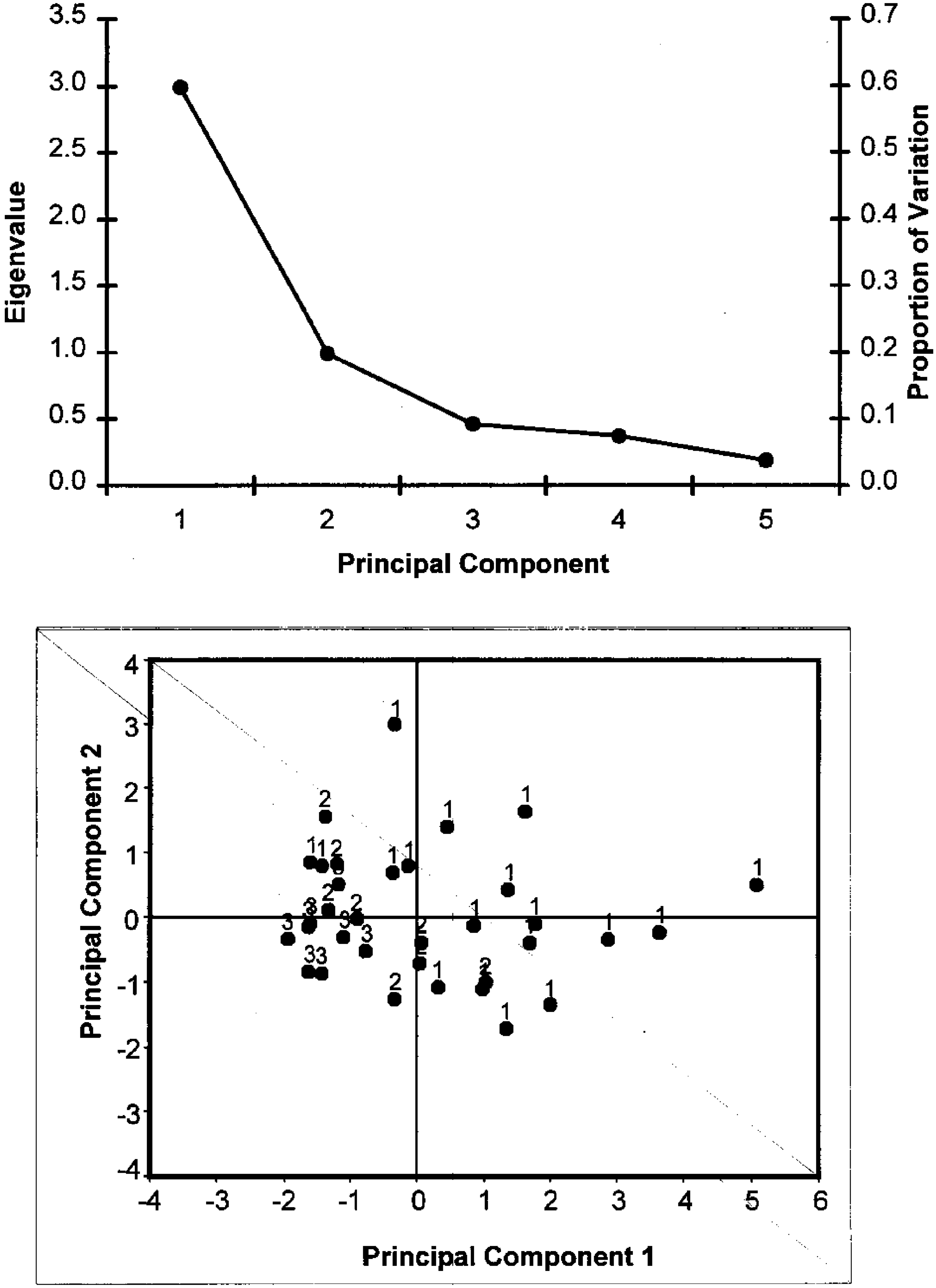

Eigenvalue
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
Proportion of Variation
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
1
2
3
4
5
Principal Component
Principal Component 2
4
3
2
1
0
-1
-2
-3
-4
-4
-3
-2
-1
0
1
2
3
4
5
6
Principal Component 1

Fig 17