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Helminth communities of ring billed gulls (*Larus delawarensis*) collected along the St. Lawrence River and Estuary

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ABSTRACT

The helminth community of ring billed gulls (*Larus delawarensis*) collected along the St. Lawrence River and Estuary.

Michael S. Levy

Twenty-nine species of helminths were found in 145 ring billed gulls collected in southern Quebec. No significant differences were observed in the helminth communities of gulls collected in May from four nesting sites (Montreal, Sorel, Quebec City, Les Pilliers), suggesting that infective pools are widespread along the St. Lawrence. Adults arriving in April had light infections. Infection levels and diversity increased during the nesting season, and over the course of the summer, due mainly to recruitment of helminths transmitted by fish. Communities in young gulls collected on the nesting island at Montreal displayed little diversity, and were dominated by *Plagiorchis multiglandularis*. Following dispersal from the colony, helminth diversity increased rapidly in young gulls. The communities in adults and juveniles were most diverse in August, at which time they were comparable. Based on the August collections, there seems to be little yearly variation in the helminth communities of adult and juvenile gulls, which tended to be more similar at the same time each year than they are at different times within a year. Infection levels and community diversity declined drastically in young gulls by November, apparently due to natural attrition of existing infections and the lack of recruitment of new ones. Ring billed gulls appear to sustain low levels of infections over winter, as suggested by the light infections seen on arrival. They quickly acquire a characteristic suite of helminth species that appears to occur commonly in gulls along the St. Lawrence.

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INTRODUCTION

Helminth parasitism is an integral part of the natural history of vertebrates. It is now well known that helminth populations are not static, nor do individual helminth species live in isolation. Their populations fluctuate, and each helminth is typically part of a larger community of parasitic species within a particular host. While helminth communities occur in all classes of vertebrate hosts, those that occur in birds, and especially those found in aquatic species, are the most diverse, this is due to their vagility, the complexity of their digestive system, their broad diet and their extensive contact with aquatic environments (Bush, Aho and Kennedy, 1990).

Although studies on the helminths of birds have appeared in the literature for many years, those focusing in detail on helminth communities are a more recent phenomenon (Bush, 1990). Bush (1990), in an insightful summary of the multitude of studies on the helminth populations of birds, identified two main problems with existing studies that limited their usefulness in contributing to a greater understanding of helminth communities. First, data from infracommunities in individual hosts from a given location (or time or age etc.) are often collapsed into some sort of summary form, then used to compare collections. These collapsed data sets are of arbitrary size and often obscure patterns that may be present in the parasite communities. The second problem is that many of the existing studies focus on a single taxon, or a particular group of helminths within a host species, providing little information about the community as a whole.

Parasite communities (which consist of populations of various species of helminths) are influenced by many factors. Some of these factors are evolutionary and

some are ecological in nature. Edwards and Bush (1989), in their paper on helminth communities in avocets, concluded that "although phylogenetic specificity is obviously important, ecological events can be equally important, and indeed overriding, in determining the composition and structure of helminth communities...". Janovy, Clopton and Percival (1992) formalized the idea by stating that "the presence, including the potential presences, of parasite species in a host species are evolutionary phenomena, whereas the parasites' population structures, including void frequency distributions, are ecological ones". Thus, while the ability of a particular helminth species to establish in a particular host species is phylogenetically determined, the population structure of those that can, and the communities that they form, are determined ecologically.

Most helminth species found in birds are acquired by ingestion of infective stages either directly from the environment, or more commonly, by the ingestion of infected intermediate hosts. Infections by schistosomes (direct penetration) and filarial nematodes (arthropod vectors) are the exception. Helminths reproduce within the definitive host but do not multiply there. Eggs are released to the external environment for further development. The only way for helminth populations to increase within the definitive host is by recruitment of new individuals. Recruitment occurs primarily by ingestion of intermediate hosts therefore factors affecting the diet of the definitive host, and / or the availability of infected intermediate hosts in the environment will have a major impact on the helminth populations and, ultimately, on the helminth community.

The complexity of the helminth community (i.e. species richness) that may develop in a particular host species is determined by a variety of factors. These include the complexity and physiology of the host digestive system, host vagility, broad host diet,

preferential feeding on intermediate hosts of a wide variety of parasites, and exposure to helminths with direct life cycles which enter by penetration (Kennedy *et al.*, 1986). Within a particular host species the gut structure and physiology can be considered constant for practical purposes. Factors associated with the diet, which may differ with age, time of year, migration status or habitat, as well as the availability of intermediate hosts are of major importance in determining the exposure to helminth populations and the communities that develop.

Host age is an important factor in determining parasite community diversity. Chicks are initially parasite free and acquire their helminths over time. Bykhovskaya-Pavlovskaya (summarized from Dogiel, 1964) performed extensive studies on the helminth fauna of various orders of birds and observed that the first group of parasites acquired by chicks tended to be cestodes. These were followed by acanthocephalans, nematodes and digeneans in sequence. She noted that in some birds, acquisition of a full suite of species occurred in as little as 1.5 to 2 weeks (see also Bush, 1990). Furthermore, mean intensity was higher in young birds than in adults. She proposed that this was due to the greater amount and variety of food consumed by the young birds.

Diet and feeding behavior are important factors in the acquisition of helminth loads in young birds. Young ducks typically have heavier infections than adults (e.g. Cornwell and Cowan, 1963; Buscher, 1965; Wallace and Pence, 1986). Ducklings are precocial and sample the environment while feeding themselves, therefore they are potentially exposed to a great number of parasites. Their heavier loads were attributed to the fact that they fed more readily on animal matter than did adults (Cornwell and Cowan, 1963).

In contrast to precocial species, nidiculous chicks, which are fed directly by the parents, are likely to have a more restricted diet consisting of locally abundant prey, thus limiting their exposure to infection. Threlfall (1968b) found that herring gull (*Larus argentatus*) chicks collected in Newfoundland as well as those collected in Northern Caernarvonshire and Anglessey (Wales) (Threlfall, 1967) were less heavily parasitised than adults. He also found that the infracommunities of adults were dominated by digeneans, whereas in chicks, cestodes predominated (Threlfall, 1968b).

Host gender has been proposed as a factor influencing helminth infections in birds, however, many authors have failed to find evidence of this. Bush (1990), after an extensive literature review, concluded that gender related differences are only found in species where different food items are consumed by the two sexes, or where different microhabitats within a specific habitat are utilized by males and females. In avian species where females and males do not differ greatly in behavioral or physical characteristics, or in diet, there is no *a priori* reason to expect gender related differences in helminth communities.

Helminth communities may vary in species that occupy different habitats during the same time of the year, or in different seasons. Differences again reflect changes in the availability of intermediate hosts and the diet of the definitive hosts. Vermeer (1969) found differences in the prevalence of two cestode species in ring billed gulls (*Larus delawarensis*) collected from two lakes in Alberta, and attributed these to dietary differences between birds in the two lakes. Bush and Holmes (1986) found that there were significant differences in the helminth communities of lesser scaup ducks (*Aythya affinis*) collected from various lakes in Alberta, but they also found that the variability

seen within lakes was almost as great as that seen between lakes. Furthermore, they demonstrated that the lake of origin was more important in determining the helminth community found in the ducks then was the ecological region in which the lake was located. Edwards and Bush (1989) found that avocets (*Recurvirostra americana*) collected from four different ponds showed significant differences in terms of the number of species and the number of helminth individuals per bird. These differences were attributed to the presence or absence of particular intermediate hosts in the ponds of origin.

Bush (1990) found significant differences in the number of helminth individuals in willets (*Catoptrophorus semipalmatus*) captured in fresh and saltwater environments. The number of species present remained fairly constant, but the relative composition of the community differed regionally. Communities in saltwater environments were dominated by digeneans, whereas cestodes and acanthocephalans dominated those in freshwater. He attributed these differences to differences in diet. Differences could certainly be anticipated in species where part of the population at a given time is associated with freshwater habitats and part with marine habitats. These differences may be attributable to differences in the availability of intermediate hosts or to ecological barriers to transmission.

Infection levels vary on a seasonal basis. Threlfall (1967) examined herring gulls in North Wales. He found that the helminths present could be classified into three categories; those that appear only in the summer, those that appear mostly in winter, and those that are present year round. These differences were attributed to changes in the diet of the gulls over the course of the year, caused by an altered availability of intermediate

hosts. Furthermore, he suggested that seasonal fluctuations in the abundance of infective stages in the environment may also play a contributing role in differences observed. In another study, Threlfall (1968b) found that seven species of helminths recovered from herring gulls in Newfoundland appeared to demonstrate seasonal variation; some helminths were most prevalent early in the summer, while others peaked in July. Furthermore, ten species also demonstrated yearly variations in prevalence.

Migratory species typically show pronounced changes in helminth infections. Hood and Welch (1980) found that red-winged blackbirds (*Agelaius phoeniceus*) underwent an increase in helminth prevalence during the breeding season. Total helminth prevalence was lowest in pre-migratory birds, and highest during incubation and feeding of the nestlings. This increase coincided with a drastic shift in diet, from one dominated by plant material to one dominated by animal matter. In waterfowl, there is a general tendency for adults to arrive on the nesting grounds with light infections. The diversity and magnitude of infection increase and peak in late summer (e.g. Busher, 1965; McLaughlin and Burt, 1973; Neraasen and Holmes, 1975). Infection levels decline throughout fall staging and migration periods, and during the stay on the wintering grounds. Generally no recruitment of replacement species occurs at this time, due to changes in diet and limited availability of infective stages in intermediate hosts (Wallace and Pence, 1986). In contrast, Bush (1990) found that willets acquired new infections on their saltwater wintering grounds and some of these persisted when the birds migrated to freshwater.

Studies on the helminth community of birds are typically carried out on common species. Although gulls as a group are abundant, surprisingly little is known of the

helminth fauna of North American species (Hair and Holmes, 1970). The only comprehensive studies of gulls in North America are those of Vermeer (1969), who examined the helminth fauna of ring billed gulls and California gulls (*Larus californicus*) in Alberta, Threlfall, who examined black-backed gulls (*Larus marinus*), kittiwakes (*Rissa tridactyla*), a glaucous gull (*Larus hyperboreus*) (1968a), and herring gulls in Newfoundland (1968b), and Hair and Holmes (1970), who examined Bonaparte's gulls (*Larus philadelphia*) in Alberta. The remaining studies deal with the taxonomy of particular helminth individuals or a particular parasitic group (e.g. Pomeroy and Burt, 1964), local surveys for a particular helminth species, or with helminth life history studies. This is in marked contrast to Europe, where the helminth fauna of gulls has received considerable attention (Threlfall, 1966, 1967; Bakke and Barus, 1975, 1976; Kennedy and Bakke, 1989; Rysavý and Sitko, 1992; Sitko , 1993).

Knowledge of the helminth community of ring billed gulls is particularly limited. Vermeer (1969) found 13 species of helminths in adult and juvenile ring billed gulls collected at Beaverhill and Miquelon lakes in Alberta. These included six digenean species (*Plagiorchis elegans*, *Diplostomum spathaceum*, *Echinostoma revolutum*, *Echinoparyphium sp.*, *Cotylurus erraticus* and *Austrobilharzia sp.*), five cestode species (*Diphyllobothrium dendriticum*, *Schistocephalus solidus*, *Paricterotaenia porosa*, *Lateriporus clerci* and *Hymenolepis californicus*), one acanthocephalan species (*Polymorphus sp.*), and one nematode species (*Aprocta turgida*). Other species of helminths have been reported from ring billed gulls, however these were in studies investigating single parasite species, or restricted parasitic groups (e.g. cestodes).

The life history of the ring billed gull is well documented (Ryder, 1993). There are two distinct breeding populations in Canada; the western interior population and the population found in the Great Lakes and St. Lawrence River basin east to coastal New Brunswick (Cramp and Simmons, 1985). The eastern and western populations remain separate during migration, with the dividing line occurring around 96°W (Root, 1988).

Spring migration begins in late February and intensifies during March. By April - May the birds have returned to the breeding grounds (Ryder, 1993). Nesting and egg laying usually occur between late April and early May. Nests are built on raised ground near water, often on beaches and islands. Incubation lasts approximately 26 days and the chicks hatch between late May and early June, although some hatch as late as early July (Ryder, 1993; Godfrey, 1986). Chicks are fed by both parents for up to 50 days. Their diet consists mostly of insects, fish and earthworms, but they are also fed small amounts of plant material, bird remains and refuse (Ryder, 1993). Chicks will also peck readily at insects (personal observation). Fledging occurs five or six weeks post hatching. At this time the young are effectively independent of parental care causing the disintegration of the family group (Ryder, 1993). Soon after fledging (mid-July and August) juveniles and adults disperse from the nesting colony to form loafing and feeding flocks in various places, including upland feeding areas such as parks and landfills (Ryder, 1993). At this time, adults and juveniles have similar diets consisting mostly of fish, arthropods, earthworms, rodents and grain. They are, however, opportunistic feeders and will eat decaying animal material, eggs and refuse (Ryder, 1993; Godfrey, 1986).

Fall migration begins in October, with pronounced changes in north-south distributions apparent by November. Typically, the gulls reach their wintering grounds by

January (Ryder, 1993). The eastern population overwinters along the Atlantic coast from New England to Mexico, mainly between the Carolinas and Florida. A small number overwinter on the Great Lakes where the waters remain open all winter long (Cramp and Simmons, 1985).

Ring billed gulls have greatly expanded their range in recent years (Godfrey, 1986). Locally, populations of ring billed gulls have increased dramatically in the St. Lawrence River basin (P. Brousseau, Canadian Wildlife Service, personal communication). Several species of helminth parasites found in gulls use fish as intermediate hosts. Some (eg. species of the digenean *Diplostomum*) are known to be pathogenic in fish. In fact, it has been shown that up to 90% of the individuals in certain species of fish in the St. Lawrence River have opaque lenses (Gagnon, Ménard and Coutu, 1992) which is an indication of *Diplostomum* sp. infections. For this reason, there is growing interest in the biology of gulls, including the identification and quantification of their helminth parasites.

The objectives of this study were:

1. to define and describe the helminth fauna of ring billed gulls in Quebec as part of a larger project on the parasites of fish-eating birds in the province,

2. to compare the helminth communities of nesting gulls at various locations along the St. Lawrence River and Estuary,

3. to monitor the development and / or change in the helminth communities of adult and young of the year gulls during the time that they are resident in Quebec,

4. to compare the communities of the different cohorts in late summer to determine whether young gulls acquire the same levels of infections as adults and,

5. and to identify species that are potential fish pathogens.

This study attempts to provide a greater understanding of the helminth communities found in ring billed gulls as well as to provide increased insight into the development of helminth communities in vagile birds with nidiculous offspring. Given the size of the ring billed gull population, they may play an important role in the dynamics of the helminth communities in fish and fish eating birds in the St. Lawrence River ecosystem.

MATERIALS AND METHODS

Definitions

As in all fields, parasite ecologists have developed specific terminology. In this thesis, the terms prevalence, abundance and intensity follow Margolis, Esch, Holmes, Kuris and Schad (1982). Prevalence is the percentage of hosts that are infected with a particular parasite species. Abundance is the total number of a particular parasite species divided by the number of hosts examined. Intensity is a measure of the number of individuals of a particular parasite species in each infected host. Mean intensity is measured by dividing the total number of worms of a particular parasite species by the number of infected hosts.

Parasite populations can be classified in a hierarchical manner. At the base of this hierarchy is the infrapopulation, which consists of all the members of a parasite species within a particular host individual. All of the infrapopulations in a particular host species within a given ecosystem are known as the metapopulation. The suprapopulation is made up of all of the forms of a parasite in an ecosystem, irrespective of host (Esch, Shostak, Marcogliese and Goater, 1990).

A parallel terminology has been developed for communities. The base of this scheme is the infracommunity, which consists of all members of all parasite species present in a given host individual (i.e. all of the infrapopulations in a single host). The combined infracommunities in a given host population are referred to as the component community. The compound community is the sum of all of the parasite communities within an ecosystem (Esch *et al.*, 1990).

Hanski (1982) developed what is referred to as the core satellite hypothesis which states that communities (in this case component communities) are made up of core and satellite species. Core species are common and abundant. They occur frequently (high prevalence) and in large numbers (high abundance). The opposite is true of satellite species. He also noted that there were many 'intermediate' species (i.e. species that were neither core nor satellite) that occurred as well. In their study on the helminth community of lesser scaup ducks, Bush and Holmes (1986) also found many intermediate species, which they designated "secondary species". Bush, Lafferty, Lotz and Shostak (1997) noted that parasitologists often misuse the terms core, secondary and satellite species to indicate prevalence. As these terms imply particular assumptions based on the metapopulation model, they were not used here. Instead helminths with a prevalence of less than 30% were considered rare species, those with a prevalence between 30% and 69% were considered intermediate species and those with a prevalence of 70% or greater as common species.

When discussing host age categories, the term chicks refers to nestlings and downy young. Juveniles are defined as fledged, young-of-the-year birds. Adults refers to birds one year old or older, although it is acknowledged that all may not be sexually mature.

Study sites and examination techniques

Gulls were collected from four nesting colonies along the St. Lawrence River and Estuary in 1994 and 1995. The colonies were located at Les Pilliers, approximately 60 km down river from Quebec City, at the Daishawa pulp and paper mill in Quebec City, Ile St. Ours near Sorel, and Ile de la Couvée at Montreal. Water conditions at these sites ranged

from estuarine at Les Pilliers to fresh at Montreal. Other gulls were collected at various locations on the Island of Montreal (Table 1).

All birds in a given collection period were collected in as short a time interval as possible to ensure a homogeneous sample, permitting valid comparisons of helminth communities (Janovy, Clopton and Percival, 1992). At least six birds were collected at each site (Edwards and Bush, 1989).

All adult gulls collected during the nesting season were nest trapped. An open-bottom wire box was positioned at an angle over the nest. One end of the box was held up by a stick with a rope attached to it. When the bird settled on the nest, the stick was pulled out causing the box to fall, thereby trapping the bird. Chicks and juveniles collected on the nesting sites were hand caught.

Birds collected in other locations were caught using a large drop net. The net consisted of a 12 by 14 foot wood frame with standard garden netting stretched across it. The net was positioned against a tall vertical surface (usually a tall fence) and controlled from behind by two lead lines connected to the upper corners of the frame. The gulls were lured to the net with bread. When the birds approached the base of the net, it was dropped, capturing the birds live.

The gulls were kept in the waterfowl holding facilities at Concordia University until examination. Preliminary studies revealed that gulls could be kept for several days without loss of worms. As a precaution, all birds were examined within two days of capture. When it was impossible to examine birds within this period, they were killed on the second day post capture and the viscera were removed, frozen in liquid nitrogen, and stored frozen until examined. Adult birds were sexed by visual examination of

reproductive organs. Chicks and juveniles could not be sexed reliably because the gonads had not developed sufficiently.

The trachea, esophagus, proventriculus, gizzard, intestine, caecae and bursa of Fabricius, when present, were removed and placed in separate Petri dishes. Each organ was opened and both the contents and the inner surface of the organs were examined for helminths with the aid of a dissecting microscope. Helminths that infect the gizzard live under the Koilin lining. Prior to examination, the gizzards were soaked in water for a few hours to facilitate the removal of the lining. Both the musculature and the inner surface of the lining were thoroughly examined for helminths.

Digeneans and cestodes were fixed in 5% buffered formalin and stored in 70% ethanol. They were prepared for microscopic examination by staining in either acetocarmine or Ehrlich's haematoxylin. Most specimens were stained in dilute acetocarmine (10 drops per 50 ml of distilled water for twelve hours). Once stained, the specimens were dehydrated in ethanol, cleared in xylene, and mounted on glass slides in Permount or Canada Balsam. Some specimens were stained in full strength Ehrlich's haematoxylin for approximately 1 hour. These specimens were differentiated in 1% HCl in 70% ethanol, blued in 1% ammonium hydroxide in 70% ethanol then dehydrated, cleared and mounted as above.

Nematodes were fixed in hot 70% ethanol, cleared in glycerin alcohol and mounted on microscope slides using glycerin jelly.

Identification of the helminths to the generic level was based on keys by Schell (1970), Yamaguti (1971) and Dubois (1968, 1970) for digeneans, Schmidt (1986) and Khalil, Jones and Bray (1994) for cestodes, and by Barus, Sergeeva, Sonin and Ryzhikov

(1978) for nematodes. Keys to species were available for some digeneans (Skrjabin, 1964; Dubois, 1968, 1970), for some cestodes (Deblock, Biguet and Capron, 1960) and for Nematodes (Barus *et al.*, 1978). The remaining species identifications were based on descriptions in the literature.

Once identified, all helminths in each host were sorted by species and counted.

Spatial comparisons

In order to compare the helminth communities at various localities along a salinity gradient, 36 adult gulls were nest trapped from four nesting colonies along the St. Lawrence River and Estuary between mid May and early June 1994. Ten birds were collected from each of three breeding colonies; Montreal (Ile de la Couveé), Sorel (Ile St. Ours) and Quebec City (Daishawa), and six birds were collected from Les Pilliers.

Comparisons within a single location

In this component of the study, gulls were collected at Ile de la Couvée during the nesting season, and at various other locations on the Island of Montreal at other times in 1994 and 1995. Ten adults were collected while on Ile de la Couvée in May, 1994 and 10 were collected in Dorval in August, 1994 following dispersal from the nesting colony. Eight adults were collected at Dorval in April 1995, prior to the onset of nesting, and an additional 15 were collected there in August 1995. Ten juvenile gulls (fledged, but still on the nesting colony) were collected from Ile de la Couvée in late June 1994 and 10 juveniles were collected in August 1994 at Dorval, concurrently with adults sampled that year. In June of 1995, 15 two - week - old chicks and 14 four - week - old chicks were

collected at Ile de la Couvée. Seventeen juveniles were collected at Dorval in August 1995, concurrently with the adult sample of that year, and 10 juveniles were collected at the Miron Dump in November of 1995. A chronological list of all the gull collections is presented in Table 1.

Data analysis

All analyses were performed using either NCSS (Number Cruncher Statistical System), SYSTAT, COMSIM, a program developed during the course of this work to calculate the various similarity indices (due to its size, the source code was not included here, however, it is available from the author), or a macro built in Microsoft Excel used to run the analysis of similarity (see Appendix 1).

Initial exploration revealed that the data were not normally distributed. All attempts to transform the data to normality failed, therefore, non - parametric tests were used. The Mann - Whitney U test was used to test for differences in total helminth load, the number of species present per host and the species abundances between the sexes of adult birds. The Kruskal - Wallis test was used to test for differences in parasite abundances and species counts between the groups of birds when more than two groups were being compared. When significant differences were detected using the Kruskal - Wallis test, Dunn's multiple comparison procedure (Hollander and Wolfe, 1973) was used in an attempt to detect where differences lay. Chi square tests of independence were used to compare the prevalence of individual helminth species between the groups of interest.

One of the major advantages of community studies carried out on parasites is that the sampling unit (the host) is a true biological unit with well defined boundaries (Aho,

1990). The host is not a sampling unit of arbitrary size or shape. When helminths are counted in a particular bird, the component parasite community of a given host population is being sampled, however, a full census of the individual host's infracommunity is also obtained. Each host is also considered a replicate sample of the local component community (Bush, 1990).

Brillouin's index was used to compare the infracommunity diversities. This index is appropriate for fully censused communities (Pielou, 1975), and it is calculated by:

$$H = \left(\log \frac{N!}{\Pi n_i!} \right) / N$$

Where H is Brillouin's index, N is the total number of worms, Π means to "take the product of" and n_i is the number of worms of species i. This index is derived from information theory (introduced by MacArthur, 1955 and Margalef, 1958) and it is related to "uncertainty". In a situation where there is high diversity, there also is high uncertainty. This implies that it becomes increasingly unlikely to correctly predict the identity (i.e. species) of a randomly chosen individual as diversity increases (Brower and Zar, 1984).

From Brillouin's index we can also calculate an eveness index which indicates how close a community is to its maximal possible diversity. The eveness index derived from Brillouin's diversity index can be compared between the various infracommunities (Pielou, 1975). The evenness index based on Brillouin's diversity index is calculated by:

$$J = H / H_{max}$$

where

$$H_{max} = \left[\log N! - (s-r) \log c! - r \log(c+1)! \right] / N$$

J is the measure of eveness, H is Brillouin's index (as above), H_{max} is the maximum possible diversity, N is the total number of worms (as above), s is the number of species present, c is the integer portion of N/s and r is the remainder portion of N/s (Brower and Zar, 1984). As these indices were normally distributed, ANOVA was used to test for differences between collections.

Infracommunities were also compared using two measures of community similarity. Jaccard's coefficient is a qualitative measure of community similarity and mean percent similarity is a quantitative measure of community similarity. Jaccard's coefficient is based solely on the presence or absence of parasite species and is therefore sensitive to rare species. Mean percent similarity is based on a comparison of the relative abundance of helminth species in the two communities. Since this index takes the abundance of individual helminth species into account it is less sensitive to rare species.

Mean Jaccard's coefficients and mean percent similarity scores, based on all pairwise comparisons within and between groupings are useful ways to summarize and compare the helminth communities, but they do not permit evaluation and comparison of individual infracommunities with each other. However, the matrices of Jaccard's coefficients or mean percent similarity scores that are generated from all pairwise comparisons are large and impossible to interpret on their own so, two methods were used to analyze and interpret them. Analysis of Similarity (ANOSIM) was used to test for statistically significant separation between groupings (i.e. for significant differences in the infracommunities of gulls from different groups) and non - metric multidimensional scaling (MDS) was used for visual interpretation of the results (Clarke, 1993).

ANOSIM is a permutation technique used to statistically test for differences between similarity scores produced by within group comparisons and those produced by comparisons of communities from different groups (i.e. collections) (Clarke, 1993). ANOSIM is based on the R statistic, which is a useful comparative measure of the degree of separation (or difference) between collections. The ANOSIM procedure begins with the calculation of all of the pairwise infracommunity similarity indices. The similarity scores are then ranked to allow the calculation of R. R is calculated by subtracting the mean rank within collections (that is the average rank of the comparisons made between birds of the same collection) from the mean rank between collections, and dividing the result by n(n-1)/4; where n is the total number of birds compared and 4 is a constant. In order to test whether the separation seen (i.e. the R value) is statistically significant, the data must be permuted (i.e. the ranks are randomly re - assigned to within and between collection comparisons) and the R statistic recalculated. This is repeated 999 times, and the number of times that the new R value is equal to or larger than the original R is recorded. This count is divided by the total number of iterations (1000) to yield the probability of achieving an R at least as large as R obtained from the original data set. If this probability is less than α then the collections are considered to be significantly different from each other.

Typically, when calculating R, the data are ranked such that the lowest rank value is assigned to the comparison with the highest similarity. Tied ranks are handled by averaging. Ranking in this manner imparts R with some interesting properties. Specifically, R ranges from -1 to 1. If $R \cong 0$ then we fail to reject the null hypothesis of no difference between the various groups. R approaches 1 as replicates within groups are

more similar to each other than replicates between groups. R is unlikely to be less than 0 because this indicates that similarities between groups are greater than those within groups.

In this study, however, the lowest rank was assigned to the comparison with the lowest similarity. Tied ranks were handled as described above. The reason for the discrepancy is that SYSTAT, which was used to rank the data, assigns ranks such that the lowest similarity score receives a rank of 1. As a consequence, R still ranges from -1 to 1, and $R \cong 0$ still causes us to fail to reject our null hypothesis however, when R approaches -1 the replicates within groups are more similar to those between groups (the same as if R approaches 1 with the other type of ranking procedure). Thus, $R > 0$ is unlikely because it indicates that replicates between groups are more similar to each other than replicates within collections. In summary, R remains a useful measure of separation but the signs are reversed from the typical situation.

While ANOSIM allows the researcher to test whether differences between groups are statistically significant, the R statistic cannot be broken down to determine where differences lie, therefore graphical methods are useful in determining which groups are responsible for the significant R value.

Non - metric multidimensional scaling (MDS) is a useful technique to graphically represent similarity matrices (Clarke, 1993). This technique takes a matrix of similarities (or dissimilarities) and generates a graph in n - dimensional space. In this case, each point represents the helminth community in a particular bird. Points that plot closer to one another are more similar to each other than to those that plot farther away. As in Principal Components Analysis, the first dimension accounts for most of the variation in the data

and subsequent dimensions account for decreasing amounts of variation. It is often sufficient to limit the plot to two (sometimes three) dimensions, which facilitates interpretation of the data. If the helminth communities of birds collected in the same location are more similar to each other than to those of birds collected in a different location, then two separate "clouds" of points would be expected to form on the plot, each cloud representing a separate location. MDS was applied to the similarity matrices for all of the pairwise Jaccard's coefficient and mean percent similarity comparisons. For the most part, the MDS based Jaccard's coefficients accounted for little of the original variation, therefore they are only reported in the text when they add to the understanding of the helminth communities.

Further analysis of the compound community was achieved using Principal Components Analysis (PCA). PCA is a multivariate technique that attempts to reduce the dimensionality of a data set. This is achieved by reducing the data to a smaller set of orthogonal components that account for most of the variation in the original data. PCA was performed on the presence and absence data as well as the covariance matrix of the $\log(x + 1)$-transformed abundance data (as suggested by Green, 1979) of all the helminths in the birds of interest in a particular analysis.

Both principal components analysis and multidimensional scaling result in values (principal components in PCA, and dimensions in MDS) that can be used to elucidate structure in the data by reducing its dimensionality. It is of interest to understand which members (i.e. species) of the infracommunities are strongly correlated with the principal components or dimensions. This information was obtained by calculating the Spearman - Rank correlations between each of the helminth species in an analysis and the dimensions

or principal components resulting from that analysis (as in Gagnon *et al.* 1992). By examining the magnitude of significant correlations and comparing these to the prevalence or abundance of that species, it is possible to gain insight into which species influence the relationship between particular infracommunities. All of the correlation coefficients are tabulated in the results, however only those that were significant were discussed in the text.

All tests were considered significant at $\alpha = 0.05$.

RESULTS

General

One hundred and forty-five gulls, including 76 young of the year (29 chicks and 47 juveniles) and 69 adults were examined. Of these, 139 individuals were infected with one to 14 helminth species; intensities ranged from one to approximately 1700 helminths per gull. A juvenile collected in August 1995 and five juveniles collected in November 1995 were uninfected. Twenty-nine species of helminths were found (Table 2). These included 10 digenean, 15 cestode, and four nematode species, of which 8, 10 and 1, respectively, were identified to the species level. With the exception of certain species in the *Wardium* complex, and to a lesser extent the *Capillaria* species, many of the unidentified helminths were found in low abundances and in few hosts. The overall prevalence and number of chicks, juveniles and adults infected by each species of helminth in the total sample is presented in Table 2. Eighteen species, including five digeneans, 11 cestodes and two nematodes, had a prevalence of less than 10% in the overall sample. Eighteen species occurred in both young and adult gulls, two occurred only in young gulls and nine occurred exclusively in adults.

Comparison of the helminth communities between the sexes

No significant differences were found in the mean number of species present, the mean helminth load, or in the prevalence or mean abundance of any helminth species in adult male and female gulls (Table 3). Accordingly, data from adult birds were pooled between the two sexes for all subsequent analyses. Comparisons were not done for young of the year birds due to the difficulty in determining the sex of the immature individuals.

Comparisons of the helminth communities between nesting sites

Details of the helminth infracommunities of gulls collected from the four nesting colonies are presented in Table 4. There was no significant difference in the mean number of helminth species found in gulls from the four colonies. Gulls from Les Pilliers had the heaviest helminth loads, due in large part to individuals with heavy infections of *Wardium cirrosa*, *Diplostomum spathaceum* ssp., and *Maritreminoides* sp. (see Table 7). Despite this, the only significant difference in total helminth loads occurred between gulls at Les Pilliers and those at Ile St. Ours (Table 4).

Helminth diversity (as indicated by Brillouin's index) was low at all four sites, but evenness values were higher (Table 4). Neither Brillouin's nor evenness scores differed significantly between the four colonies.

The proportion of digeneans, cestodes, and nematodes in the component communities of gulls at each of the nesting sites is shown in Table 5. Digeneans dominated the helminth communities of gulls at Daishawa and at Les Pilliers whereas cestodes were predominant, although to a lesser extent, in the communities from Ile de la Couvée and Ile St. Ours. Nematode infections were rare or absent at each of the nesting colonies.

Twenty - seven species were identified from the nesting gulls. Six species were found in gulls at all four of the nesting sites; eight, three and 10 species were found in gulls at three, two, and one site respectively (Tables 6 and 7). Significant differences were found in the prevalence of *Maritreminoides* sp., *W. cirrosa*, *Wardium* sp.1, *C. obvelatus*, and *Capillaria* sp.1 (Table 6). The abundances of *D. spathaceum*, *Maritreminoides* sp.,

W. cirrosa, *C. obvelatus*, and *Capillaria* sp.1 also differed significantly between the four nesting colonies (Table 7). With the exception of the prevalence of *Wardium* sp.1, there was a general tendency for species showing significant differences between the nesting colonies to have higher prevalences and abundances in gulls from the downriver sites (Daishawa and Les Pilliers).

The numbers of common, intermediate and rare species present in the component communities of gulls collected from each of the nesting colonies are presented graphically in Figure 1. Only two common species were identified; *D. spathaceum* was a common species in the communities at all of the nesting sites. *Wardium* sp.1 was a common species in the communities of gulls collected on Ile de la Couvée, and was the second most prevalent species at Ile St. Ours and Daishawa. Curiously, it was not found in gulls from Les Pilliers. There were comparable numbers of intermediate and rare species in the component communities of gulls at Ile de la Couvée, Ile St. Ours and Daishawa, however, there were more intermediate and fewer rare species at Les Pilliers.

Mean Jaccard's coefficients and mean percent similarity scores, performed on all pairwise combinations, were used to compare the average similarity between the helminth communities in gulls from the four nesting colonies (Table 8). The within colony mean Jaccard's scores were similar at all four nesting colonies. Mean percent similarity scores were more variable with the highest scores occurring in communities at Daishawa. The mean Jaccard's scores for between colony comparisons involving Ile de la Couvée, Ile St. Ours and Daishawa were similar. Those that included comparisons with Les Pilliers were lower. Within colony similarity scores for a given nesting site were always greater than those resulting from comparisons between them and Les Pilliers. Conversely, the highest

between colony mean percent similarity score was between Daishawa and Les Pilliers. There was extensive overlap in all of the similarity scores. The large standard deviations suggest that the infracommunities are as variable within nesting sites as they are between sites.

Analysis of similarity on the mean percent similarity scores revealed no significant separation between the four nesting sites ($R = -0.002$, $P = 0.89$). When the mean percent similarity matrix for all pairwise comparisons among the four sites was subjected to non-metric multidimensional scaling, the first three dimensions explained nearly 44.8% of the variation in the data. Three species were significantly correlated with the first, five with the second and five with the third dimension resulting from the analysis (Table 9). Species that were negatively correlated with the first dimension either occurred exclusively in the downriver colonies, or were most abundant there (Tables 7 and 9). *Wardium* sp.1 (the only helminth with a positive correlation on the first dimension) was more abundant in the upriver sites. Species with positive correlations on the second dimension tended to be either particularly abundant or conspicuously missing from the Daishawa collection. Species with negative correlations with the second dimension were less abundant in the downriver sites. Correlations with the third dimension did not appear to be related to location of the nesting colonies.

The distribution of the infracommunities based on the MDS analysis are shown in Figure 2. There was no tendency for the helminth communities in gulls from particular nesting colonies to form distinct groupings. Each group overlapped to a greater or lesser extent with the others, further suggesting that the variability in helminth communities of gulls from different nesting colonies is no greater than that from a single colony. The six

birds that did separate from the rest included at least one bird from each of the four nesting sites. These seemed to differ mostly due to factors associated with the second dimension. This dimension was strongly negatively correlated with the abundance of *Wardium* sp.1. This species was absent from Les Pilliers, but was common at Ile de la Couvée, Ile St. Ours and, to a lesser extent, at Daishawa (Tables 7 and 9).

Results of the principal component analyses performed on the presence or absence data are shown in Table 10 and Figure 3. The first two principal components accounted for 47.9% of the variation in the data. Spearman rank correlations of each of the helminth species on each of the first two principal components revealed that seven species were significantly correlated with PC1 and nine species were correlated with PC2 (Table 10). *Diplostomum spathaceum*, *W. stellorae* and *Wardium* sp.1 had positive correlations with PC1. These species occurred in high prevalences in at least three of the collections (Tables 6 and 10). *Cosmocephalus obvelatus*, *A. brevis*, *W. cirrosa* and *Capillaria* sp.1, which were negatively correlated with PC1, occurred either exclusively or in relatively high prevalences at Les Pilliers. Eight species; *A. brevis*, *S. denticulata*, *Maritreminoides* sp., *W. cirrosa*, *D. lateralis*, C. *obvelatus*, *Capillaria* sp.1, and *Capillaria* sp.2, all of which occured exclusively or were most prevalent at Les Pilliers were positively correlated with PC2. *Wardium* sp.1 and *Wardium* sp.2, which were both absent from Les Pilliers, were negatively correlated with PC2.

A plot of the two principal components derived from this analysis is shown in Figure 3. The infracommunities did not form distinct groups based on the location of nesting colonies from which the gulls were collected. There was extensive overlap among the infracommunities, especially those of gulls from Ile de la Couvée, Ile St. Ours and

Daishawa. Infracommunities from the gulls from Les Pilliers overlapped those from other collections, but to a much lesser extent.

Principal components analysis on the covariance matrix of the log(x+1)-transformed abundance data resulted in two components which accounted for 53.7% of the variation in the data. The first component was positively correlated with the abundance of *D. spathaceum*, which was most abundant at Les Pilliers, and *S. denticulata*, which was most abundant at Daishawa (Tables 7 and 11). Positive correlations were observed between the abundance of *W. stellorae* and *Wardium* sp.1 and PC2. These were among the most abundant species at Ile de la Couvée and Ile St. Ours. *Diplostomum spathaceum*, *A. brevis*, which was most abundant at Daishawa, *Maritreminoides* sp., *W. cirrosa*, *C. obvelatus*, and *Capillaria* sp.1, all of which were either found exclusively at or were most abundant at Les Pilliers, and *D. lateralis*, which was most abundant at Ile St. Ours were negatively correlated with PC2.

The plot of first two principal components is shown in Figure 4. As in the previous analysis, there was extensive overlap among helminth infracommunities between nesting colonies. PC1 was not useful in separating groups due to the large range of values for this component. There was a tendency for infracommunities from Les Pilliers to have higher values on PC1 and lower values for PC2. This caused partial separation between infracommunities from Les Pilliers and those from Ile de la Couvée and Ile St. Ours. The main cause of this separation appeared to be the relatively high abundance of *D. spathaceum*, *Maritreminoides* sp., *W. cirrosa*, *C. obvelatus*, and *Capillaria* sp.1 present at Les Pilliers and the higher abundance of *W. stellorae* at Ile de la Couvée.

Comparison of the helminth communities of adult gulls collected at Montreal

The details of the helminth infracommunities of ring billed gulls collected at Montreal prior to, during and following the nesting season are presented in Table 12. Despite different sample sizes, equal numbers of helminth species were recovered from gulls collected at each of the collection times. The mean number of helminth species per bird did not differ significantly between the four collections, however, the mean number of helminths per bird was significantly greater in the August 1994 collection than in the April 1995 collection.

Neither Brillouin's index nor evenness scores differed significantly between the four collection times (Table 12). Brillouin's scores indicated low species diversity at each of the collection times, but evennesss values indicated near maximal diversity at each of the four sites, given the number of helminth species recovered.

The relative proportions of digeneans, cestodes, and nematodes in the compound communities are summarized in Table 13. Cestodes dominated the parasite community in April and to a lesser extent in June, but digeneans dominated the parasite community in August. Nematodes were approximately as common as digeneans in April, but were rare in the other collections.

Adult gulls harbored 23 helminth species. Of these, five were found in all four collections, eight were found in three collections, four were found in two collections and six were found in one collection (Tables 14, 15). The prevalence of *D. spathaceum*, *M. pricei*, *P. multiglandularis*, and *Capillaria* sp.1 differed significantly between the four collection periods (Table 14). The prevalence of *Capillaria* sp.1 was greatest in April; the prevalence of the other species showing significant differences were higher in June or

August. The abundance of these same four species also differed significantly between the four periods (Table 15). The pattern seen in the abundances of these species was identical to that seen for the prevalences.

The number of common, intermediate and rare species in the component communities is shown in Figure 5. There were no common species in the April collection. *Diplostomum spathaceum* (June, August 1994), *P. multiglandularis* (August 1994 and 1995) and *Wardium* sp.1 (June) were the only common species identified in the other collections. Comparable numbers of intermediate and rare species were found in all four collections.

Mean Jaccard's coefficients and mean percent similarity scores for the four collections are presented in Table 16. The April collection had the lowest within collection scores for both indices, and comparisons that included this group resulted in lower scores than did comparisons among the other collections. The two August collections had the highest between collection scores, suggesting a greater similarity between communities at the same time between years than at different times within the same year.

ANOSIM using the mean percent similarity scores revealed significant separation between the collections ($R = -0.047$, $P = 0.001$). Though the degree of separation between sites was statistically significant, the low R value suggests that the separation was slight. Unfortunately, the R statistic cannot be broken down mathematically to carry out *post hoc* multiple comparisons to detect where the differences lie. The first three dimensions obtained from the MDS on the matrix of mean percent similarities accounted for 43.8% of the variation in the data set. *Wardium* sp.1 had a positive correlation with

the first dimension, and it was least abundant in April (Tables 15 and 17). The abundances of *W. stellorae* and *D. lateralis* were negatively correlated with the first dimension. These two species tended to be most abundant in April and June. *Mesophorodiplostomum pricei*, *Echinostoma* sp. and *P. multiglandularis*, which were all rare or nearly absent from the April collection, and which were substantially more abundant in one or both of the August collections, showed a positive correlation with the second dimension. *Wardium stellorae* and *Capillaria* sp.1, which tended to be most abundant in April and June, were negatively correlated with the second dimension. *Diplostomum spathaceum*, *M. pricei* and *P. multiglandularis*, which were all absent or nearly so in April, were positively correlated with the third dimension. The only negative correlation on the third dimension involved *Wardium* sp.2, which was most abundant in April and was absent in August 1994.

The results of the MDS on the mean percent similarity matrix are shown in Figure 6. There were no distinct groupings based on collection period, however, only three birds from the April and June collections had values which were positive for dimension two. This, combined with the fact that eight of the 10 birds collected in August 1994 had positive values for the second dimension, seems to have created some separation between the early summer collections and the one from August 1994. The infracommunities from the August 1995 collection were dispersed more or less evenly in all three dimensions.

Principal components analysis on the presence or absence data resulted in two principal components which explained 39.7% of the variation in the original data (Table 18). *Wardium* sp.1, which was most prevalent in the June collection and was approximately equally prevalent in the other three collections, was positively correlated

with PC1 (Tables 14 and 18). *Wardium stellorae*, which was most prevalent in June, *D. lateralis*, which was absent from the two August collections and *S. denticulata*, which was least prevalent in June, were all negatively correlated with PC1. *Plagiorchis multiglandularis* and *Echinostoma* sp., which were most prevalent in one or both of the August collections, were positively correlated with PC2. *Wardium stellorae* and *Capillaria* sp.1, which was most prevalent in April, were negatively correlated with PC2.

The two principal components resulting from the analysis of the presence or absence data are plotted in Figure 7. There was extensive overlap of infracommunities and no distinctive groups formed on the basis of the collection period.

The first two principal components resulting from the PCA on the abundance data explained 53.3% of the variation in the data (Table 19). All three of the species which had positive correlations with PC1 were digeneans which were conspicuously absent, or present in low abundances, in the April collection (Table 15 and 19). With the exception of *D. spathaceum*, which was most abundant in June, their numbers peaked in August 1994. *Wardium* sp.2, *Aploparaxis* sp., *M. ductilis* and *T. cylindraceus* were most abundant in early summer and were all positively correlated with PC2. There were no negative correlations between the abundance of any of the helminth species and either of the components.

The plot of the first two principal components is shown in Figure 8. Though extensive overlap of the infracommunities was evident, there appeared to be slight separation between the April and June collections. Most of the collections have a wide range of values for PC1, however none of the April infracommunities had a score greater than approximately 0.02. In addition, most of the infracommunities in the June sample had

scores for PC2 which were greater than 0.1. All but one of the April infracommunities plotted below this value. These results suggest that the separation shown in the ANOSIM was probably caused by a difference in the infracommunities of the April sample and those of the other samples. The August collections were quite variable and overlapped with many of the other infracommunities.

Comparison of the helminth communities of juvenile gulls collected at Montreal

Significant differences occurred among the helminth infracommunities of young gulls collected throughout the year at Montreal (Table 20). In general, the total number of helminth species recovered and the mean number of species per bird were low in chicks, were greatest in August, then declined sharply by November. Only five of the ten gulls examined in November were infected. The mean number of helminths per bird peaked in the four - week old gulls, however only the number in the November collection differed significantly.

Mean Brillouin's diversity scores were low when the birds were two weeks old (Table 20). These remained low in June then peaked in August. By November they had dropped to significantly lower levels. Evenness scores showed the same trend, however the November decline, though still significant compared to August, was not as pronounced as it was for the diversity indices.

Table 21 shows the proportion of digeneans, cestodes and nematodes in the component communities of the young gulls. The communities were dominated by digeneans except in August 1994 when cestodes predominated. Nematodes were rare in most of the collections and were absent in the November collection.

None of the 20 species of helminths recovered from the young gulls occurred in all six collections. Four species were recovered in five collections, one in four collections, seven in three collections, one in two, and seven in one collection (Table 22 and 23).

Significant differences were seen in the prevalence of *D. spathaceum*, *C. platycephalus*, *P. multiglandularis*, *S. denticulata*, *W. stellorae*, *Wardium* sp.1, *Wardium* sp.2, *C. obvelatus* and *Capillaria* sp.2 (Table 22). The abundance of these same species also differed significantly between the six collections (Table 23). With the notable exception of *P. multiglandularis*, which was significantly more abundant in June than in August or November, the tendency was for the prevalence and abundance of those species that showed significant differences to increase over the course of the summer and decline sharply by November.

The numbers of common, intermediate, and rare species recovered from the juveniles are shown in Figure 9. *Plagiorchis multiglandularis* was a common species in the June and August 1994 collections; both *P. multiglandularis* and *D. spathaceum* were among the most prevalent species in August 1995.

The mean Jaccard's coefficient and mean percent similarity scores are presented in Table 24. The three June collections had particularly high within and between collection scores, indicating strong similarity between the helminth infracommunities. The August collections had lower within collection similarity scores when compared with the June collections. The similarity scores between the August collections were greater than the within collection scores for August 1995, suggesting that individual variation in communities examined at the same time between years was not as great as that from communities sampled at various times within the same year. The November collection had

very low within collection scores, and generated equally low scores when compared to other collections.

ANOSIM revealed significant separation between the six collections. This occurred when either the Jaccard's coefficients ($R = -0.097$, $P = 0.001$) or the mean percent similarity scores ($R = -0.098$, $P = 0.001$) were examined. The first two dimensions obtained from the MDS of the Jaccard coefficients accounted for 30.4% of the variation in the data set (Table 25). *Plagiorchis multiglandularis*, which was most prevalent in the three June collections and absent from the November collection, was positively correlated with the first dimension (Tables 22 and 25). *Diplostomum spathaceum*, *A. brevis*, *S. denticulata*, *W. stellorae*, *C. porosa* and *Capillaria* sp.1, were all negatively correlated with the first dimension. These species were most prevalent in one or both of the August collections and, with the exception of *Capillaria* sp.1, were the only species present in November. *Cotylurus platycephalus*, which was most prevalent in the two August collections, was positively correlated with the second dimension. *Cosmocephalus obvelatus*, *Capillaria* sp.1, and *M. pricei* were negatively correlated with the second dimension. These species were absent from the November collection and were most abundant in one, or both of the August collections.

A plot of the first two dimensions obtained demonstrated that the infracommunities of chicks and fledged juveniles in June, tended to have positive values for the first dimension (Figure 10). This was caused by the high prevalence of *P. multiglandularis* in these collections. The November collection formed a sparse group that separated from the others apparently due to the absence of nematodes and *M. pricei*. Infracommunities of

the four - week - old chicks seemed to form a boundary between the infracommunities of chicks and those of the August collections, which tended to overlap extensively.

The first two dimensions derived from the MDS on mean percent similarity scores accounted for 41.4% of the variation in the data (Table 26). The abundance of *P. multiglandularis*, which was greatest in June, was positively correlated with the first dimension (Tables 23 and 26). This dimension was negatively correlated with *D. spathaceum*, *A. brevis*, *Echinostoma* sp., *S. denticulata*, *W. stellorae*, *Wardium* sp.2, *C. porosa* and *C. obvelatus*, all of which were most abundant in one of the August collections, and absent, or nearly so, from the June and November collections. *Diplostomum spathaceum*, *A. brevis*, *S. denticulata*, and *C. obvelatus* were positively correlated with the second dimension; *W. stellorae* was negatively correlated with the second dimension.

The MDS plot on mean percent similarity scores (Figure 11) demonstrated that most of the helminth infracommunities of birds collected at the nesting colony (i.e. the collection of two - week - old, four - week - old and fledged juveniles) had positive values for the first dimension. This was caused by the high abundance of *P. multiglandularis* in these collections. These collections were almost completely separated from the two August and the November collections. Fairly extensive overlap was seen between the August and November collections. Thus, the separation demonstrated by the ANOSIM was due to the separation of the three June collections from the rest.

The first two components derived from the analysis on the prevalence data accounted for approximately 60% of the variation in the data. The first principal component was positively correlated with *P. multiglandularis*, *C. obvelatus* and *Wardium*

sp.1 (Table 27). *Echinostoma* sp., which was only present in the August 1995 collection, *P. porosa*, and *Wardium* sp.2 were negatively correlated with PC1. The second principal component was also positively correlated with *P. multiglandularis*, and was negatively correlated with *D. spathaceum*, *M. pricei*, *A. brevis*, *S. denticulata*, *P. porosa*, *C. obvelatus* and *Capillaria* sp.1.

Figure 12 is a plot of the two principal components derived from this analysis. Two clusters of points representing the infracommunities of birds were immediately apparent. One cluster was made up of all of the infracommunities of young gulls collected in June as well as some of those collected in August. This cluster separated from the rest by having values for PC1 which were greater than 0.13 and by having mostly positive values for PC2. This group apparently reflects the high prevalence of *P. multiglandularis* and the low prevalence of *D. spathaceum* in the June collections. The infracommunities of the gulls collected in August and November had values of less than 0.13 on PC1 and had mostly negative values for PC2, apparently reflecting the relatively lower prevalence of *P. multiglandularis* and the higher prevalence of *D. spathaceum* at these times.

The first two principal components derived from PCA on the abundance data accounted for approximately 68% of the variation in the data (Table 28). *Plagiorchis multiglandularis* and *Wardium* sp.1were positively correlated with PC1 and *D. spathaceum* and *Wardium* sp.2 were negatively correlated with this component. *Plagiorchis multiglandularis*, and *C. platycephalus* were positively correlated with PC2 whereas *D. spathaceum*, *S. denticulata*, *Wardium* sp.1, and *Wardium* sp.2 were negatively correlated with this component.

A plot of the principal component scores revealed a distinct separation between the June and November samples (Figure 13). As with previous comparisons, the August collection overlapped those of both June and November, with the August 1995 communities appearing less variable than those of August 1994.

Comparison of the helminth communities of adults and juveniles collected in August of different years

Details of the helminth infracommunities of adult and juvenile gulls collected from Montreal in August of 1994 and 1995 are presented in Table 29. There was no significant difference in the mean number of species in birds belonging to the different cohorts collected in the same year or between gulls of the same age between years. Similarly, no significant differences were seen in the mean helminth loads between these groups.

The Brillouin's scores and evenness scores were virtually identical in the juvenile samples, and both scores were similar to those obtained in the 1994 adult sample (Table 29). Although both scores obtained in the 1995 sample were lower, neither differed significantly from those of the other groups.

The relative composition of the helminth component community of both age groups in August of each year is shown in Table 30. With the exception of the communities in juveniles collected in 1994, which were dominated by cestodes, digeneans predominated. Nematodes were rare in all of the collections, however they consistently formed a greater percentage of the communities of juveniles.

Twenty-one species of helminths were found in adult and juvenile gulls. Four species were found only in juveniles, three of which were found in only one year. Four

other species were found only in adults and three of those were also found only in one year. (Tables 31 and 32).

Significant differences were found in the prevalences of *P. multiglandularis*, *Wardium* sp.1, *Wardium* sp.2, *C. obvelatus*, and *Capillaria* sp.2 (Table 31). *Plagiorchis multiglandularis* and *Wardium* sp.1 were consistently more prevalent in adults. On the other hand, *C. obvelatus* was more prevalent in juveniles. *Capillaria* sp.2 and *P. multiglandularis* were more prevalent in 1994 than in 1995; the opposite was true of the prevalence of *Wardium* sp.2.

The abundances of the same five species differed significantly between the four collections; *P. multiglandularis* and *Wardium* sp.1 were more abundant in adults than juveniles, *C. obveatus* was more abundant in juveniles than adults, *Wardium* sp.1 and *Capillaria* sp.2 were more abundant in 1994 than 1995, and *Wardium* sp.2 was more abundant in 1995 than 1994 (Table 32). Dunn's multiple comparison procedure was only able to detect differences in the abundance of *P. multiglandularis*.

The number of common, intermediate, and rare species in the communities of adult and juvenile gulls collected in August is presented in Figure 14. Only two common species were identified. *Plagiorchis multiglandularis* was a common species in all of the collections except the juveniles collected in 1995, where it was one of the intermediate species. *Diplostomum spathaceum* was a common species in both of the 1994 collections, but a intermediate species in the two 1995 collections.

Mean community similarity scores are shown in Table 33. Adults had consistently higher within collection scores than did juveniles collected in the same year. Scores for both age groups in 1994 were consistently greater than those for 1995. Most of the

between collection scores were smaller than the within collection scores. In general, the helminth communities of ring billed gulls collected in August tended to be similar, irrespective of age or year of collection.

ANOSIM on mean percent similarity scores revealed no significant separation between the four collections (R = 0.004, P = 0.57). The first three dimensions of the MDS on mean percent similarity scores explained only 36.1% of the variation in the data (Table 34). *Diplostomum spathaceum*, *S. denticulata*, and *Wardium* sp.1 were positively correlated with the first dimension, however, no clear pattern of abundance was evident; some were most abundant in adults and others in juveniles (Tables 32 and 34). *Diplostomum spathaceum*, *M. pricei*, *W. stellorae*, *A. brevis* and *C. obvelatus*, were positively correlated with the second dimension, and again no pattern in abundance was evident. *Wardium stellorae* and *Wardium* sp.2, were negatively correlated with the first dimension. *Diplostomum spathaceum*, *M. pricei*, *A. brevis*, and *C. obvelatus* were positively correlated with the second dimension. This dimension was negatively correlated with *Echinostoma* sp., *W. stellorae* and *Wardium* sp.1. The third dimension was positively correlated with *Echinostoma* sp. and *P. multiglandularis*. Negative correlations occurred between the third dimension and *W. stellorae*, *Wardium* sp.1 and *Capillaria* sp.2.

The plot of the three dimensions of the MDS analysis is shown in Figure 15. There was extensive overlap between each of the four groups and no separation of any particular group was evident.

Principal components analysis based on the presence or absence of helminths in the infracommunities of adult and juvenile gulls produced two components that accounted for

47.8% of the variation in the data (Table 35). The first component was positively correlated with the presence of *D. spathaceum*, *A. brevis*, *S. denticulata*, *P. multiglandularis* and *Wardium* sp.1. *Wardium* sp.2 was the only species negatively correlated with PC1. The second principal component was positively correlated with *D. spathaceum*, *A. brevis*, *Wardium* sp.1 and *C. obvelatus*. *Wardium stellorae* was the only species with a negative correlation on PC2.

The plot of the first two principal components is shown in Figure 16. Overlap of the infracommunities was extensive and no groupings based on the age of the gull hosts or on the year of collection could be identified.

The first two principal components resulting from the PCA on the abundance data explained 51.9% of the variation in the data (Table 36). *Diplostomum spathaceum*, *M. pricei*, *A. brevis*, *S. denticulata*, *P. multiglandularis* and *Wardium* sp.1 were all positively correlated with PC1. *Wardium* sp.2 was the only species that was negatively correlated with PC1 (Table 36). *Diplostomum spathaceum* and *M. pricei* were positively correlated, and of *W. stellorae* was negatively correlated with PC2.

The plot of the first two principal components resulting from this analysis is shown in Figure 17. Again, there was extreme overlap and the infracommunities did not appear to separate on the basis of age group or collection year, however, the infracommunities in adults from 1995 appeared to show greater variability than did the other collections. These results support the ANOSIM; there did not appear to be any significant differences in the infracommunities of gulls collected in August, regardless of the age of the birds, or the year of collection.

DISCUSSION

Taxonomy and life history

Twenty-nine species of helminths were recovered in this study. Of these 19 were identified to the species level. Two digeneans could not be identified to the species level because of the poor quality of the material or because they were immature.

Five cestodes, including three belonging to the genus *Wardium*, were not identified to species. There appears to be a complex of species in *Wardium* that has not been adequately defined in the literature. While the species present in our sample could be readily distinguished on the basis of cirrus and vaginal morphology, adequate descriptions of these features are not available. A major problem centers on the fact that some of these species were described 50 to well over 100 years ago and, although the original descriptions are adequate to identify the cestodes to the level of this complex, they are not sufficiently detailed to permit species level identification. This group of species will require a thorough revision (ideally based on the original material, if it still exists) before this problem is resolved. Generic level identifications were based on Schmidt (1986) despite the fact that more recent revisions of the hymenolepidid and dilepidid cestodes appear in Khalil *et al.* (1994). This latter work includes many revisions at the generic level but no updated species lists were provided. The single specimens of *Diphyllobothrium* and *Aploparaxis* were too poorly preserved to allow for specific identification.

Three nematode species (*Tetrameres* sp., *Capillaria* sp.1 and *Capillaria* sp.2) could not be identified because only females were recovered and males are necessary for positive species identification. It is probable that the two *Capillaria* species are in fact the same. *Capillaria* sp.1 was found in the gizzard and *Capillaria* sp.2 was found in the

esophagus. They are very similar morphologically, and as the anterior portion of the digestive tract was kept in water, sometimes for as long as 24 hours while the intestine was examined, it is possible that esophageal forms may have migrated into the gizzard. The decision to designate them as different species was based on the belief that it was better to treat them separately than to collapse them into a potentially heterogeneous group. It should be noted that "the classification of the Capillariinae is one of the most difficult and unsatisfactory in the Nematoda" (Anderson, 1992), therefore the older, more established generic name was retained in this study.

Although not all species could be named, certain generalizations regarding their life histories are possible because there is little variation in the life history patterns within genera. Digeneans all require a snail intermediate host and most require second intermediate host as well. The life cycles of *Diplostomum*, *Mesophorodiplostomum*, *Cardiocephalus*, *Cotylurus*, *Apophallus* and *Stephanoprora* use fish as second intermediate hosts. *Echinostoma* uses snails, *Maritreminoides* uses freshwater arthropods, and *Plagiorchis* uses the aquatic larvae of insects (Yamaguti, 1975). In the case of *P. multiglandularis*, gulls may acquire infections by eating the infected insect larvae while foraging in aquatic habitats, or by eating the adult insects once they have emerged.

Among cestodes, *Diphyllobothrium* sp. (and likely *Tetrabothrius*) require fish as second intermediate hosts (Wardle and McLeod, 1968). *Ophryocotyle proteus* is transmitted by polychaetes (Burt, 1962). The dilepidid species in gulls, specifically *Anomotaenia micracantha* and *A. dominicanus*, use marine amphipods as intermediate hosts (Jarecka, Bance and Burt, 1984); no information on the life history of *C. porosa* is

present in the literature. Among the hymenolepids, species of *Aploparaxis* are transmitted by aquatic oligochaetes, and species of *Wardium*, *Microsomacanthus*, and *Drepanidotaenia* (at least those found in anatids) are transmitted by a range of copepod and ostracod species (McDonald, 1969). Cysticercoids of *M. ductilis* occur in marine amphipods (Burt and Jarecka, 1984), but there is no information available on the intermediate hosts of other hymenolepidids infecting gulls.

Cosmocephalus obvelatus is transmitted by amphipods (Wong and Anderson, 1982), *Tetrameres* species are transmitted by a range of arthropods, and *Capillaria* species have direct life cycles, however earthworms can also be involved (McDonald, 1969; Anderson, 1992).

With the exception of *Capillaria* and *Plagiorchis*, which can be transmitted in terrestrial habitats, all of the helminth species recovered from gulls are transmitted through aquatic hosts, primarily fish and arthropods.

Species of *Diplostomum* are known to be pathogenic in fish (Chappell, 1995) but virtually nothing is known regarding the potential pathogenesis of the other digeneans in fish. Due to their extensive populations, gulls likely play a major role in the transmission of these parasites. *Diphyllobothrium* is also a known pathogen in fish, however, infections were so rare that it is unlikely that gulls contribute in a significant way to infection levels of this parasite in fish of the St. Lawrence River.

Data analysis

Analysis of the different types of data (i.e. similarity matrices, raw abundance counts and presence or absence data) provided comparable results. Though the actual

results varied between the MDS and comparable PCA (i.e. analyses dealing either with presence and absence or with abundance), the interpretation of the results led to similar conclusions. However, some features emerged from the analyses that bear comment. First, low values of R in ANOSIM, while significant, were difficult to interpret. This was evident in the data on adult gulls at Montreal but was not a problem with larger values of R (see the juvenile comparisons). Secondly, it was evident that PCA analyses on species presence or absence data or MDS on Jaccard's coefficients, were less informative than were analyses on abundance data. In all cases the amount of explained variation was greater (often substantially so) in the latter analyses. The reason is that analyses based on abundance data are less sensitive to rare species than are those based purely on presence and absence. Furthermore, the abundance data automatically includes information about the prevalence of the helminths (i.e. an abundance greater than zero indicates that the helminth was present).

PCA has successfully been used in other studies to compare the helminth communities of different species of hosts (Stock and Holmes, 1987; Alexander and McLaughlin, 1997). To the best of our knowledge however, this is the first use of ANOSIM and MDS in the analysis of helminth communities. These techniques have been used in other of studies (Clarke, 1993), but never in parasite ecology. Although there are some limitations, ANOSIM and MDS are potentially useful tools to compare helminth communities.

General

As gulls are opportunistic feeders and do not specialize on any particular prey item, it was not surprising to find that many of the species recovered occurred relatively rarely. Twenty-nine species were recovered and on average, each gull had 3.4 ± 2.2 species. This is comparable to the results obtained by Kennedy and Bakke (1989) who recovered 33 species of helminths, and found a mean of 3.3 species per bird from common gulls (*Larus canus*) in Norway. Threlfall (1968a,b) recovered 35 species of helminths from herring gulls,14 species from great black-backed gulls (*Larus marinus*), five from kittiwakes (*Rissa tridactyla*) and four from glaucous gulls (*Larus hyperboreus*) in Newfoundland, and Hair and Holmes (1970) found seven species in their study on Bonaparte's gulls (*Larus philadelphia*) in Alberta, however the mean number of species per bird was not reported in these studies.

Vermeer (1969) recovered six digenean, five cestode, one acanthocephalan and one nematode species from 46 adult and 40 juvenile ring billed gulls in Alberta. In this study we found 29 species of helminths; 10 digeneans, 15 cestodes, and four nematodes but no acanthocephalans. However, only two species found by Vermeer (*D. spathaceum* and *C. porosa*) were recovered in this study, which suggests that substantial differences exist between the diversity of the infective pools present in the two sites. Helminths found in ring billed gulls in this study were typically gull parasites and in most cases occur in a variety of gull species in eastern North America (e.g. Threlfall 1968 a,b; Pomeroy and Burt, 1964). At least some of the helminths found in Alberta occur in a variety of duck species (e.g. *Echinostoma revolutum*, *Echinoparyphium* sp. (cf. *recurvatum*, *flexum*), *Cotylurus erraticus* and *Lateriporus clerci*) (McDonald, 1969). It appears that ducks had

a major impact on the infective pools in the lakes examined by Vermeer (1969). This is not the case along the St. Lawrence River.

Overall, individual gulls examined in this study harbored few species. The mean number of species per bird in this study ranged from 1.2 (in the two-week-old birds) to 6.3 (at Les Pilliers) and a maximum of 14 species was found in a single gull collected at Les Pilliers. The intensity of infection levels varied widely; the mean number of helminths ranged from 7.7 in infected gulls in Montreal in November to 555.2 in nesting birds at Les Pilliers. With few exceptions (notably the collections of chicks in June and juveniles in November, both of which had extremely low diversity and evenness scores) mean Brillouin's diversity scores ranged from 0.27 to 0.45, which is comparable to the 0.18 to 0.65 reported for the mean Brillouin's index scores in common gulls by Kennedy and Bakke (1989), but lower than those reported by other studies on other birds, such as grebes (Stock and Holmes, 1987), avocets (Edwards and Bush, 1989), willets (Bush, 1990) and ducks (Alexander and McLaughlin , 1997). It seems that gulls typically have lower helminth diversity than other aquatic birds, likely due to their generalist feeding behaviour. Mean evenness scores ranged from 0.38 to 0.66, indicating that although the helminth diversity in gulls is moderate, it approaches the maximum possible diversity, given the number of helminths present.

The number of common species identified was low compared to that found in other studies on other species of birds (e.g. Bush and Holmes, 1986; Stock and Holmes, 1987). The wide variety of foods eaten by gulls likely accounts, in part, for this. Species specializing on particular prey are more likely to come in contact with parasites transmitted by that prey, resulting in high prevalence and abundance of the particular

parasite. Generalist feeders like gulls, which in addition to having a broad diet also forage extensively on land, would have less opportunity for infection by most species. Three species seemed to be particularly important in defining the helminth community of ring billed gulls. *Diplostomum spathaceum*, *Wardium* sp.1 and *P. multiglandularis* were either common species or at least among the most prevalent species in almost all of the collections. Interestingly, these are transmitted (or are presumed to be transmitted) by three different types of intermediate hosts; fish, crustaceans and semi-aquatic insects, respectively.

Comparison of the helminth communities between adult males and females

Studies on other bird species have reported differences in levels of infection in males and females. These were generally attributed to differences in diet caused by alterations in behavior or nutritional requirements brought on by rearing offspring (summarized in Bush, 1990). Differences in infection levels in males and females should only be found in hosts where females and males feed on different food items, or use different microhabitats within a specific habitat (Bush, 1990). Neither of these situations are known to be the case for ring billed gulls, and there are no known differences in their dietary habits (Ryder, 1993). As their exposure to parasitic infective stages is likely to be similar, it was not surprising that overall infection levels and the prevalence and abundance of individual species in females and males was similar. Threlfall (1968a) found no significant differences in the infections of male and female black backed gulls, however in another study (1968b), he stated that the intensity of eight of the 35 species in differed

between genders. Unfortunately no data or explanation was provided, and it is not certain whether the infections in one sex were consistently different from those in the other.

Comparison of the helminth communities between nesting sites

Differences in the prevalence or abundance of a particular species of helminth in a given location, or at a given time, is a reflection of the availability of intermediate hosts, the existence and extent of the infective pool and the frequency of exposure of individual hosts to that pool. As all of the common species were found in gulls from most or all of the nesting colonies, it is evident that infective pools are widespread along the St. Lawrence River.

Gulls begin to arrive on the upper St. Lawrence in late March. Breeding pairs (and probably many non breeding individuals as well) persist locally for several months, although it is probable that there is also considerable movement of gulls at this time. Adult gulls may sample different environments before actually settling on a nesting colony. During this period they will acquire parasites from existing infective pools as they become available (e.g. digeneans in fish), and presumably establish, then draw from the new infective pools (e.g. hymenolepidid cestodes) as they develop. Many of the helminths found in this portion of the study may actually have been acquired before nesting began. Under these circumstances it is not surprising that communities from the different locations are similar, particularly when a relatively small number of species, using a limited number of transmission patterns, are involved.

While no significant differences were detected between the helminth communities at each of the nesting colonies, virtually all of the analyses suggested that those from Les

Pilliers were somehow different from the rest. There were a number of unusual features observed in the helminth communities from Les Pilliers. The range and mean number of helminth species and the mean number of helminth individuals recovered per bird, as well as the standard deviations of both of these were greater in the collection from Les Pilliers than from any of the other three nesting sites. These factors contributed to the low diversity and evenness scores seen for this collection. In general however, few differences were observed in either the prevalence or abundance of the different helminth species recovered at the different nesting sites. Communities at Les Pilliers had comparable numbers of common species, but nearly twice as many intermediate species as in the nesting colonies. With the exception of the mean percent similarity score with Daishawa, community similarity scores between Les Pilliers and the other sites decreased with increasing distance upriver, perhaps reflecting differences in the helminth communities present along the environmental gradient present between Ile de la Couvée and Les Pilliers. The Jaccard's coefficients suggested that the relative prevalence of helminth species was similar between the four collection sites but mean percent similarity scores seemed to reflect slight differences in the relative abundance of helminth species between sites. In some instances the between collection scores were higher than the within collection scores (e.g. between Daishawa and Les Pilliers or with scores involving Ile St. Ours). Bush (1990) found a similar situation in willets and suggested that the greater between group scores were due to the uneven distribution of individual helminth species, which may have be caused by one of two mechanisms; either some definitive hosts were selectively preying upon infected intermediate hosts, or the distribution of infective stages may have been aggregated in the intermediate host population.

Analysis of similarity, supported by MDS analysis of mean percent similarity and the two PCA analyses, demonstrated that the four nesting sites did not differ significantly in terms of their helminth communities. However, examination of the correlations between the helminth species and the dimensions or principal components, revealed that the strongest correlations tended to occur with species that were either more prevalent or more abundant at upriver or downriver sites.

The lack of significant differences between the communities of nesting gulls makes any discussion of putative differences speculative, however, some observations are warranted. It is first important to recognize that the variability within and between colonies was extensive. It follows from the within colony variation that the variability between individuals was also high, and that the variability at Les Pilliers was particularly extreme.

Virtually all of the helminths found at Les Pilliers also occurred at other nesting sites despite the fact that the colony was located in the estuary. Initially, it was expected that helminths with marine life cycles would be present in this sample. Some (*M. ductilis*, *A. dominicanus* and *T. cylindraceus*) were found, but only in low numbers. Almost all of the species recovered are normally transmitted by freshwater intermediate hosts, although a few may also infect anadromous fish (e.g. *Diplostomum*, *Diphyllobothrium*) and are available to gulls in estuarine environments. While it is possible that other species may be transmitted in estuarine conditions, a more likely scenario is that ring billed gulls move regularly from the estuary to inland freshwater bodies, which become infection foci for a greater or lesser number of helminth species. If this is the case, gulls frequenting particular wetlands could acquire particular species or develop different infection levels.

Both Vermeer (1969) and Bush and Holmes (1986) found differences in helminth infections associated with the lakes that particular samples came from. However, Bush and Holmes (1986) also noted that helminth communities of lesser scaup ducks collected at a given lake were nearly as variable as communities collected at different lakes.

The number of intermediate species was higher in the component community at Les Pilliers than at the other three sites. Thus, the prevalence of several species was greater here than at the other nesting sites. Greater prevalences and abundances reflect increased frequency of contact with populations of infected intermediate hosts. A possible explanation for the increased contact with populations of intermediate hosts lies in the fact that Les Pilliers was the most remote site studied. Each of the other three sites were in close proximity to urban centers of varying size and agricultural areas. There are no urban centers around Les Pilliers, although agricultural activity occurs. This may force gulls from Les Pilliers to eat more 'natural' food. Gulls feeding more extensively on natural food (i.e. aquatic prey items) would likely acquire heavier helminth loads than gulls at other nesting locations. Furthermore, gulls depending on natural food would spend more time sampling the natural environment, which would also increase contact with all species, including the less common ones. This may, perhaps, explain the tendency for heavier infections and the presence of more intermediate species at Les Pilliers.

The foregoing notwithstanding, the major item of interest is the fact that the communities were so similar in adults from nesting sites along the river. It is evident that most gulls at this time of year have been exposed to the same range of species regardless of nesting location.

Comparison of helminth communities of adult gulls collected at Montreal

Studies on various species of birds have shown that helminth infections tend to decline during fall migration and reach their lowest levels in winter. Although some birds acquire new species on the wintering grounds (see Bush, 1990), others (e.g. blackbirds and waterfowl) apparently do not (Hood and Welch, 1979; Wallace and Pence, 1986). Examination of adult gulls in June and August 1994, and in April and August 1995, provided an opportunity to examine seasonal changes over a 12 month period and to compare infection levels in late summer (when they should be highest) in successive years.

There is no way of knowing where the population of gulls caught in April overwintered and, as gulls were present in the Montreal area for nearly a month before the collections were made, it is not certain to what extent the communities in April reflect the those on the wintering grounds. With the exception of *T. cylindraceus*, all of the species found in April are thought to be transmitted by freshwater intermediate hosts. Based on this data, it appears that ring billed gulls either do not acquire marine species while on their wintering grounds, or if they do, apparently loose them by April.

Gulls collected in April 1995 harbored significantly fewer helminths than gulls in August 1994. Otherwise there were no differences in the infracommunity parameters of gulls collected at different times of the year, or between gulls in August of successive years. Within group community similarity comparisons revealed that there was extensive variation with each sample that seemed to be constant, regardless of collection period. Infracommunities in the April sample were most dissimilar, reflecting the low prevalence

and abundance of the species present, and this was also reflected in the between group comparisons with other collection periods.

While there were few numerical differences between the communities, there were large differences in the species composition of the April community when compared to the others. ANOSIM revealed significant separation between the four groups. The MDS and PCA analyses, and their associated correlations indicated that the April collection was different from the others.

The communities in April were dominated by cestodes and eight of the 13 species found in adult gulls were present in this group. Four of the five species not recovered were only found once at other times, thus gulls in April already have almost the full complement of cestode species. Whether these cestode species persisted through the winter, were recruited on the wintering area, or were recruited locally earlier in the spring is unknown. Nematode infections were prominent and the prevalence and abundance of *C. obvelatus* and *Capillaria* sp.1 were greatest at this time. With the exception of *S. denticulata*, the paucity of digeneans was the most striking feature of the April sample. Five of the digenean species found in gulls at Montreal use fish as second intermediate hosts and the low prevalence of these parasites suggests that fish are not available to gulls in April, or that few fish are infected at this time.

The major changes that occurred in the helminth communities centered around increased levels of digenean infections, especially *D. spathaceum* and *P. multiglandularis*, and to a lesser extent, the decline or disappearance of a number of cestode species. The increase in most of the digenean infections appeared to reflect an increase in the amount of fish (or aquatic insects in the case of *P. multiglandularis*) in the diet of the gulls. Infection

levels of some of the cestodes, notably *W. stellorae*, *Wardium* sp.1 and *C. porosa*, remained relatively constant whereas other species declined or disappeared. Most of the latter species occurred infrequently. Some (e.g. *T. cylindraceus*, *M. ductilis* and *A. dominicanus*) are transmitted in marine conditions, and eventually disappear from birds in freshwater, apparently due to the lack of suitable intermediate hosts. Others perhaps occur so infrequently that they are unable to establish locally. The disappearance of *C. obvelatus* and *Capillaria* sp.1 in June was striking, given the prevalences seen in April. As the nematodes have different life cycles, there is no common explanation why this occurred and it may simply be a sampling artifact.

The results of this portion of the study indicate that adult gulls return to the St. Lawrence River each spring with helminth communities dominated by cestodes, and a striking lack of digeneans transmitted by fish. Over the course of the summer the numbers of cestodes decline, and some species disappear. There was a shift to a digenean-dominated community. The infracommunities present in gulls collected in August were the most diverse. Little is known about the summer movements of gulls. Extensive movements by the gulls could contribute to the increased diversity of the communities seen later in the summer, as a result of parasites acquired in different habitats.

Ring billed gulls collected in August of successive years displayed some differences in the prevalence and abundance of particular species. Some differences were expected. Despite this, it is evident that the helminth communities in gulls collected in August of successive years are similar.

Comparison of the helminth communities of juvenile gulls collected at Montreal

Young birds hatch free of helminth infections. Most begin to acquire infections immediately. The rate, magnitude and sequence of species acquired will vary depending on diet and feeding behavior. Typically, infection levels increase rapidly throughout the summer and peak before declining in the fall. The decline, if there is one, is due to loss of individuals without replacement, resulting from dietary or spatial changes that restrict exposure to new infections. Examination of young gulls produced an opportunity to follow the development of the helminth community, compare the infection levels in late summer (when they should be highest) in two consecutive years and, concurrently, and to compare the infection levels of young of the year and older gulls.

In contrast with the adult sample, significant differences were observed between collection periods in all of the infracommunity parameters. Two-week-old birds examined in June had few species, light loads and the lowest diversity index and evenness scores of any group. As expected, the infection levels rose over the course of the summer with most parameters reaching maximum levels in August, before declining precipitously in November. Only half of the gulls examined in November were infected and those that were harbored only one or two species. This decline was apparently due to the loss of parasites through natural attrition and lack of replacement due, most likely, to diminished availability of intermediate hosts in late fall. The general pattern of helminth infections in young ring billed gulls is similar to that reported in other migratory species (e.g. summary in Dogiel, 1964; Busher, 1965; Bush, 1990).

ANOSIM revealed significant separation of the communities between the six collection periods. The results of the MDS and PCA analyses were nearly identical and

clearly showed that the communities in young gulls in June were similar to each other and quite different from the rest. The reason for this was the heavy infections of *P. multiglandularis*, which was present in every bird examined in June. *Plagiorchis multiglandularis* formed the overwhelming proportion of the helminth loads in these birds, producing low diversity and evenness scores, as well as the high within and between similarity scores seen in these samples. *Plagiorchis multiglandularis* is transmitted by insects. Metacercariae are present in nymphs of mayflies and other aquatic insects and become available during the massive hatches that occur in June around Montreal. During this period, enormous numbers are available to the chicks and, as a consequence, every chick was infected, usually with large numbers of this fluke. The prevalence of *P. multiglandularis* was still high in the August but the mean abundance had declined significantly, and it had disappeared from the samples by November.

Other digeneans were rare in the two- and four-week-old birds. Those species that were present are transmitted by fish, and they occurred primarily in fledged birds. Most of these species occurred more frequently and in greater numbers in the August sample, and had disappeared from the November sample.

There are three possible explanations for the apparent lack of digeneans transmitted by fish in the June collections. First, it is possible that adult gulls do not feed fish to the chicks. Possibly, other types of food are easier to catch, or are more plentiful near the nesting colony at this time. Secondly, it is possible that the chicks are in fact fed fish, but that the infective stages are less viable after having spent longer periods in the parents fore gut. This may cause excessive exposure to digestive enzymes and acid conditions; first in the parent gut and then in the chick gut. A third possibility is that the

food items may pass too quickly through the gut, due to its reduced size in chicks, thereby limiting the window of opportunity for the helminths to establish in the intestine.

Cestode infections were rare in two of the June samples, but several species, including *W. stellorae* and *Wardium* sp.1 were present in several of the four-week-old birds - sometimes in large numbers. The presence of cestodes in this group indicates that infective pools were available close to the nesting colony, and that young gulls had contact with them. The life cycles of these species are not known but based on the life cycles of congenerics that infect anatids, copepods and ostracods likely serve as intermediate hosts (McDonald, 1969). Levels of cestode infections peaked in August although there was some variability (sometimes significant) between years. The infection levels of *C. obvelatus*, and to a lesser extent the *Capillaria* species, followed a similar pattern. With the exception of the *Capillaria* species, which have direct life cycles and which may in fact be transmitted more effectively in terrestrial habitats, the increase noted in the infection levels of the cestodes and *C. obvelatus* reflects increased contact with aquatic crustaceans. Amphipods, which transmit *C. obvelatus*, are large enough to be selected as food items but copepods and ostracods are likely to be eaten accidentally while the gulls forage for larger prey.

Juvenile gulls eventually acquired all of the digenean and nematode species found in the adults, however, only six species of cestodes (compared to 13 in adults) were found. Five species were found in chicks in June, while they were still on the nesting colony. As these were clearly local birds, local transmission of the parasites occurred. *Ophryocotyle proteus* was found in one juvenile in 1995 at Montreal. This cestode is transmitted by polychaetes (Burt, 1962) and thus has a marine or estuarine life cycle. Bush (1990) found

this cestode in adult willets in Alberta during the summer and considered it a relic of the marine fauna acquired during the winter. The presence of this cestode and of *H. leptosoma*, a digenean also thought to be transmitted in marine conditions, in a juvenile collected locally is noteworthy. Either these helminths can be transmitted locally (i.e. in freshwater conditions, possibly by a paratenic host) or the birds in question had been in contact with marine or estuarine conditions indicating that the movements of juvenile gulls are far more extensive than presently believed.

As with the adults, there was no difference in the overall infection levels or in the helminth communities of juvenile gulls examined in August 1994 and 1995. Like the adults, it appears that the community of helminths in young gulls is similar from year to year although infection levels by individual species may differ. The basic diet of gulls will remain constant from year to year, and as a consequence helminth infections should remain comparable as well.

Interestingly, there were no differences found in the infection levels of adults and juveniles collected in August of the same year. Adult gulls have established infections when the chicks hatch; the latter acquire their infections *de novo*. Young gulls acquire infection levels comparable to those in adults by August. As juvenile and adult gulls have similar diets (Ryder, 1993) and feed in mixed flocks, there is no reason to expect qualitative differences in their infection levels. The fact that young gulls began life uninfected but acquired comparable infection levels to adults by August, suggests that they accumulated parasites more rapidly than adults during this period.

Overview

Twenty-nine helminth species were identified from ring billed gulls in Quebec. Most species found were characteristic gull parasites and, for the most part, are restricted to this group. The majority of the species recovered are transmitted in freshwater. Seven species; five digeneans and two cestodes are transmitted by fish. At least two (*Diplostomum* and *Diphyllobithrium*) are known to be pathogenic in fish (Schaperclaus, 1991; Chappell, 1995). There is no evidence to suggest that gulls share helminths of other fish eating birds. Whether species in gulls can infect other bird hosts awaits further study.

Ring billed gulls typically harbored few parasite species. Diversity indices tended to be low; evenness indices tended to be higher. Similarity indices indicated that within and between sample variation was high and variation in community similarity indices was often as great within as it was between communities, due to the generalist type of feeding behavior of gulls. Common species were rare, again, possibly due to the broad diet of the gull hosts. *Diplostomum spathaceum*, *Plagiorchis multiglandularis* and an unidentified *Wardium* species were the only common species identified.

Assuming that the same degree of similarity occurs between communities at different times of the year as they do in August, the following scenario is envisaged. Adult gulls return to Quebec with light infections consisting mostly of cestodes. Evidence from juvenile birds in November and the August 1994 samples indicated that there was a substantial decline in infection levels over fall and winter. Infections in gulls returning in April represented species acquired over the winter, during spring migration, or shortly after arrival on the St. Lawrence. Infection levels, especially by digenean species transmitted by fish, were low and increased between April and the onset of the nesting

season. Helminth communities in gulls from various locations along the river, however, were similar regardless of the ecological zone in which the nesting colony was located. Infection levels, especially those of digeneans, tended to increase until August in adults but some species, notably cestodes, declined or disappeared. This may have been due to natural attrition of species with marine life cycles or, perhaps, species that occur to infrequently to establish infective pools successfully. A few adults in August still harbored marine species. It was not clear, however, whether these were infections that had persisted in local birds, or whether infected birds were immigrants from marine or estuarine habitats.

There was no indication that helminth communities in adults change from year to year, however, prevalences and abundances of individual species varied significantly.

Chicks acquired heavy infections of *Plagiorchis multiglandularis* while still at the nesting colony and this species dominated the helminth communities in these birds . As they became more independent and left the colony, young gulls acquired other digeneans, cestodes and nematodes. By August they had acquired infection levels comparable to those in adults. No differences were noted in the communities of juveniles in August 1994 or 1995 nor were differences noted between cohorts collected in the same year.

Infection levels declined sharply by November and by the time freeze up forced the gulls to migrate they had lost virtually all of their infections. Sometime during early spring the gulls acquired new infections (primarily cestodes) that were present in the gulls in April.

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Table 1. Summary of the collections made at various localities along the St. Lawrence River and Estuary. The number of birds collected is indicated by n and age is defined as in the text. Comparisons refers to which comparisons the birds were involved in; geographical (G), progression of helminth communities from chicks to juveniles (P), seasonal comparisons of adults (S), and comparisons between adults and juveniles in August (A).

Locality	Date	n	Age	Comparisons
Montreal	May 17, 1994	10	Adult	G, S
Sorel	May 19, 1994	10	Adult	G
Quebec	May 25, 1994	10	Adult	G
Les Pilliers	June 6, 1994	6	Adult	G
Montreal	June 22, 1994	10	Juvenile	P
Montreal	August 18 - Sept 3, 1994	10	Adult	S, A
Montreal	August 18 - Sept 3, 1994	10	Juvenile	P, A
Montreal	April 8 - 12, 1995	8	Adult	S
Montreal	June 20, 1995	15	Chick (2 weeks)	P
Montreal	June 30, 1995	14	Chick (4 weeks)	P
Montreal	August 21 - 26, 1995	15	Adult	S, A
Montreal	August 21 - 26, 1995	17	Juvenile	P, A
Montreal	November 8 - 14, 1995	10	Juvenile	P

Table 2. Overall prevalence of helminth species recovered from 145 ring billed gulls collected along the St. Lawrence River and Estuary.

Parasite	Overall Prevalence (%)	Number Infected		
		Total	Adults	Juveniles
Digeneans				
Diplostomum spathaceum ssp.	46.9	68	49	19
Mesophorodiplostomum pricei	14.48	21	14	7
Cardiocephalus medioconiger	2.76	4	1	3
Cotylurus platycephalus	2.07	3	1	2
Apophallus brevis	21.38	31	20	11
Echinostoma sp.	6.90	10	8	2
Himasthala leptosoma	1.38	2	1	1
Stephanoprora denticulata	30.34	44	29	15
Maritreminoides sp.	2.07	3	2	1
Plagiorchis multiglandularis	56.55	82	29	53
Cestodes				
Wardium stellorae	32.41	47	30	17
W. cirrosa	4.14	6	5	1
W. clavicirrus	1.38	2	2	0
Wardium sp.1	35.17	51	37	14
Wardium sp.2	11.03	16	7	9
Wardium sp.3	0.69	1	1	0
Microsomacanthus charadrii	4.14	6	6	0
M. ductilis	3.45	5	5	0
Drepanidotaenia lateralis	3.45	5	5	0
Aploparaxis sp.	1.38	2	2	0
Ophryocotyle proteus	0.69	1	0	1
Anomotaenia dominicanus	7.59	11	11	0
Choanotaenia porosa	17.93	26	19	7
Tetrabothrius cylindraceus	2.76	4	4	0
Diphyllobothrium sp.	0.69	1	1	0
Nematodes				
Cosmocephalus obvelatus	25.52	37	13	24
Tetrameres sp.	0.69	1	0	1
Capillaria sp.1	11.03	16	10	6
Capillaria sp.2	5.52	8	4	4

Table 3. Comparison of the helminth infections in adult male and female ring billed gulls collected along the St. Lawrence River and Estuary.

Parasite	Females (n = 31)		Males (n = 38)	
	Prevalence (%)	Mean Abundance (S.D.)	Prevalence (%)	Mean Abundance (S.D.)
Digeneans				
Diplostomum spathaceum ssp.	64.5	11.2 (18.6)	76.3	39.5 (73.2)
Mesophorodiplostomum pricei	25.8	4.4 (12.3)	15.8	0.5 (1.4)
Cardiocephalus medioconiger	3.2	0.03 (0.2)	-	-
Cotylurus platycephalus	-	-	2.6	0.03 (0.2)
Apophallus brevis	19.4	2.6 (9.6)	36.8	4.7 (12.1)
Echinostoma sp.	19.4	9.1 (25.6)	5.3	1.2 (6.5)
Himasthala leptosoma	-	-	2.6	0.3 (1.6)
Stephanoprora denticulata	32.2	2.4 (7.8)	50.0	5.8 (17.4)
Maritreminoides sp.	-	-	5.3	37.0 (227.9)
Plagiorchis multiglandularis	51.6	15.2 (36.1)	34.2	26.6 (128.3)
Cestodes				
Wardium stellorae	45.2	9.7 (21.1)	42.1	6.3 (17.0)
W. cirrosa	6.4	2.0 (7.6)	7.9	16.0 (91.7)
W. clavicirrus	3.2	0.1 (0.7)	2.6	0.3 (1.6)
Wardium sp.1	51.6	9.7 (16.1)	55.3	11.3 (21.8)
Wardium sp.2	12.9	1.2 (4.8)	7.9	1.2 (4.6)
Wardium sp.3	3.2	0.1 (0.5)	-	-
Microsomacanthus charadrii	12.9	2.6 (10.2)	5.3	1.4 (8.0)
M. ductilis	3.2	0..6 (3.2)	10.5	1.9 (9.9)
Drepanidotaenia lateralis	6.4	0.2 (1.1)	7.9	0.2 (0.6)
Aploparaxis sp.	3.2	0.03 (0.2)	2.6	0.1 (0.7)
Anomotaenia dominicanus	12.9	0.5 (1.6)	18.4	0.6 (1.6)
Choanotaenia porosa	22.6	0.6 (1.5)	31.6	0.9 (1.8)
Tetrabothrius cylindraceus	3.2	0.03 (0.2)	7.9	0.1 (0.5)
Diphyllobothrium sp.	-	-	2.6	0.03 (0.2)
Nematodes				
Cosmocephalus obvelatus	16.1	0.2 (0.6)	21.0	0.5 (1.4)
Capillaria sp.1	9.7	0.3 (1.1)	18.4	0.4 (0.9)
Capillaria sp.2	3.2	0.03 (0.2)	7.9	0.2 (0.7)
Mean number of species (S.D.)	4.3 (1.7)		4.8 (2.4)	
Mean total helminth load (S.D.)	73.1 (62.7)		157.0 (328.4)	

Table 4. Comparison of the helminth infracommunities in adult ring billed gulls collected at the four nesting colonies along the St. Lawrence River and Estuary.

	Ile de la Couvée	Ile St. Ours	Daishawa	Les Pilliers
No. examined	10	10	10	6
Total # species	15	15	15	18
Mean # species / bird (SD)	4.4 (2.3)	4.5 (2.5)	4.2 (1.3)	6.3 (4.0)
Range of species	2 - 8	1 - 7	2 - 6	3 - 14
Mean # worms / bird (SD)	64.6 (63.8)	44.7 (35.6)[1]	76.8 (64.9)	522.2 (644.2)[1]
Range of # worms	7 - 171	6 - 120	2 - 200	44 - 1700
Mean Brillouin's Index (SD)	0.33 (0.17)	0.35 (0.20)	0.34 (0.14)	0.27 (0.10)
Mean Eveness score (SD)	0.66 (0.25)	0.64 (0.27)	0.62 (0.24)	0.38 (0.13)

Note: Values with a superscript ([1]) are significantly different from each other (determined by Kruskal-Wallis analysis of variance and Dunn's multiple comparison procedure).

Table 5. Composition of the helminth component communities of adult ring billed gulls collected at the four nesting colonies along the St. Lawrence River and Estuary.

	Ile de la Couvée	Ile St. Ours	Daishawa	Les Pilliers
Total	646[1]	447	768	3133
	100[2]	100	100	100
Digenea	288	162	664	2383
	44.6	36.2	86.4	76.06
Cestoda	358	285	101	731
	55.4	63.8	13.2	23.33
Nematoda	0	0	3	19
	0	0	0.4	0.61

1 - Number of worms in each taxon; 2 - Percent of total (%).

Table 6. The prevalence (% birds infected) of the helminth species recovered from ring billed gulls collected at the four nesting colonies along the St. Lawrence River and Estuary.

Parasite	Ile de la Couvée	Ile St. Ours	Daishawa	Les Pilliers
Digeneans				
Diplostomum spathaceum ssp.	80	90	90	83
Mesophorodiplostomum pricei	30	20	30	-
Cardiocephalus medioconiger	10	-	-	-
Cotylurus platycephalus	-	-	10	-
Apophallus brevis	30	20	20	67
Echinostoma sp.	-	10	-	-
Himasthala leptosoma	-	-	10	-
Stephanoprora denticulata	20	30	50	50
***Maritreminoides* sp.**	-	-	-	33
Plagiorchis multiglandularis	-	20	40	17
Cestodes				
Wardium stellorae	50	50	40	33
W. cirrosa	-	10	20	50
W. clavicirrus	-	-	-	17
***Wardium* sp.1**	70	60	50	-
Wardium sp.2	20	10	20	-
Wardium sp.3	10	-	-	-
Microsomacanthus charadrii	20	10	10	33
M. ductilis	20	10	-	17
Drepanidotaenia lateralis	10	20	-	33
Aploparaxis sp.	10	-	-	-
Anomotaenia dominicanus	-	10	20	50
Choanotaenia porosa	40	30	10	33
Tetrabothrius cylindraceus	20	-	-	17
Diphyllobothrium sp.	-	-	-	17
Nematodes				
Cosmocephalus obvelatus	-	-	20	67
***Capillaria* sp.1**	-	-	-	33
Capillaria sp.2	-	-	10	17

Note: Species names in **bold** indicate that significant differences exist between the four nesting colonies.

Table 7. The mean abundance (and standard deviation) of the helminth species recovered from adult ring billed gulls collected at the four nesting colonies along the St. Lawrence River and Estuary.

Parasite	Ile de la Couvée	Ile St. Ours	Daishawa	Les Pilliers
Digeneans				
***Diplostomum spathaceum* ssp.**	24.0 (38.1)	9.0 (10.3)[1]	41.5 (52.1)	155.8 (109.4)[1]
Mesophorodiplostomum pricei	2.1 (5.6)	1.8 (5.4)	0.7 (1.2)	-
Cardiocephalus medioconiger	0.1 (0.3)	-	-	-
Cotylurus platycephalus	-	-	0.1 (0.3)	-
Apophallus brevis	2.0 (5.3)	3.2 (7.0)	35.6 (6.0)	4.5 (6.1)
Echinostoma sp.	-	0.1 (0.3)	-	-
Himasthala leptosoma	-	-	1.0 (3.2)	-
Stephanoprora denticulata	0.6 (1.3)	1.0 (2.0)	4.2 (7.1)	2.2 (3.5)
***Maritreminoides* sp.**	-	-	-	234.3 (573.5)
Plagiorchis multiglandularis	-	1.1 (2.8)	16.8 (34.1)	0.3 (0.8)
Cestodes				
Wardium stellorae	13.0 (27.2)	4.6 (8.2)	1.8 (3.2)	6.0 (10.3)
W. cirrosa	-	3.8 (12.0)	-	100.7 (227.9)
W. clavicirrus	-	-	-	1.7 (4.1)
Wardium sp.1	10.5 (12.1)	10.6 (13.0)	3.8 (5.7)	-
Wardium sp.2	0.9 (2.0)	0.3 (0.9)	3.3 (8.3)	-
Wardium sp.3	0.3 (0.9)	-	-	-
Microsomacanthus charadrii	7.7 (17.4)	0.5 (1.6)	0.1 (0.3)	8.2 (20.0)
M. ductilis	1.9 (5.7)	6.1 (19.3)	-	1.8 (3.0)
Drepanidotaenia lateralis	0.2 (0.6)	0.9 (2.0)	-	0.3 (0.8)
Aploparaxis sp.	0.1 (0.3)	-	-	-
Anomotaenia dominicanus	-	0.6 (1.9)	1.0 (2.2)	1.3 (1.8)
Choanotaenia porosa	0.8 (1.2)	1.1 (2.0)	0.1 (0.3)	1.5 (2.8)
Tetrabothrius cylindraceus	0.4 (1.0)	-	-	0.2 (0.4)
Diphyllobothrium sp.	-	-	-	0.2 (0.4)
Nematodes				
Cosmocephalus obvelatus	-	-	0.2 (0.4)	1.3 (1.2)
***Capillaria* sp.1**	-	-	-	1.2 (1.8)
Capillaria sp.2	-	-	0.1 (0.3)	0.7 (1.6)

Note: Species names in **bold** indicate that significant differences exist between the four nesting colonies. Cells within the same row that have a superscript ([1]) are significantly different from each other.

Table 8. Mean Jaccard's coefficients and mean percent similarity scores for the helminth communities in adult ring billed gulls collected from the four nesting colonies along the St. Lawrence River and Estuary. These were calculated from all of the possible pairwise comparisons within and between collections.

Jaccard's Coefficients (S.D.)

	Ile de la Couvée	Ile St. Ours	Daishawa	Les Pilliers
Ile de la Couvée	27.2 (21.4)	0.28 (0.18)	0.24 (0.15)	0.16 (0.16)
Ile St. Ours	26.9 (22.7)	20.6 (20.7)	0.28 (0.19)	0.18 (0.16)
Daishawa	28.5 (23.2)	27.8 (24.5)	44.8 (23.8)	0.20 (0.14)
Les Pilliers	18.4 (22.0)	20.5 (24.0)	34.8 (28.8)	29.7 (30.2)

Mean percent similarity (S.D.)

Table 9. Spearman Rank correlations between each of the helminth species and the first three dimensions resulting from non-metric multidimensional scaling of the mean percent similarity scores of adult ring billed gulls collected at the four nesting colonies along the St. Lawrence River and Estuary.

	Dimension 1	Dimension 2	Dimension 3
Percent of variation explained	21.4	13.3	10.1
Digeneans			
Diplostomum spathaceum ssp.	- 0.76[1]	0.20	0.22
Mesophorodiplostomum pricei	-0.19	0.00	-0.06
Cardiocephalus medioconiger	0.17	0.23	0.25
Cotylurus platycephalus	-0.22	0.06	0.10
Apophallus brevis	-0.02	0.46[1]	-0.50[1]
Echinostoma sp.	0.25	-0.14	-0.04
Himasthala leptosoma	-0.24	0.07	-0.09
Stephanoprora denticulata	-0.14	0.46[1]	-0.22
Maritreminoides sp.	-0.05	0.30	-0.22
Plagiorchis multiglandularis	0.01	0.11	-0.33[1]
Cestodes			
Wardium stellorae	0.14	0.27	0.72[1]
W. cirrosa	-0.11	0.32	-0.41[1]
W. clavicirrus	-0.02	0.15	-0.25
Wardium sp.1	0.34[1]	-0.80[1]	-0.10
Wardium sp.2	-0.07	-0.33[1]	-0.26
Wardium sp.3	0.15	-0.25	-0.17
Microsomacanthus charadrii	-0.03	-0.11	-0.49[1]
M. ductilis	-0.07	-0.08	-0.25
Drepanidotaenia lateralis	0.26	0.44[1]	-0.25
Aploparaxis sp.	0.15	-0.25	-0.17
Anomotaenia dominicanus	0.00	0.07	-0.22
Choanotaenia porosa	-0.03	-0.05	-0.17
Tetrabothrius cylindraceus	-0.05	-0.07	-0.18
Diphyllobothrium sp.	-0.12	0.10	0.22
Nematodes			
Cosmocephalus obvelatus	-0.38[1]	0.28	-0.14
Capillaria sp.1	-0.22	0.14	-0.14
Capillaria sp.2	-0.19	0.24	-0.10

Note: correlation coefficients with a superscript ([1]) are significant.

Table 10. Spearman Rank correlations between each of the helminth species and the first two components resulting from the principal components analysis of the presence or absence data from adult ring billed gulls collected at the four nesting colonies along the St. Lawrence River and Estuary.

	Principal component 1	Principal component 2
Percent of variation explained	31.7	16.2
Digeneans		
Diplostomum spathaceum ssp.	0.51[1]	0.11
Mesophorodiplostomum pricei	-0.11	-0.13
Cardiocephalus medioconiger	0.06	0.25
Cotylurus platycephalus	0.16	0.18
Apophallus brevis	-0.44[1]	0.68[1]
Echinostoma sp.	0.14	-0.24
Himasthala leptosoma	-0.20	0.28
Stephanoprora denticulata	0.01	0.74[1]
Maritreminoides sp.	-0.29	0.36[1]
Plagiorchis multiglandularis	-0.20	-0.06
Cestodes		
Wardium stellorae	0.70[1]	0.08
W. cirrosa	-0.46[1]	0.44
W. clavicirrus	-0.24	0.27
Wardium sp.1	0.51[1]	-0.71[1]
Wardium sp.2	-0.10	-0.46[1]
Wardium sp.3	-0.02	-0.22
Microsomacanthus charadrii	-0.20	-0.04
M. ductilis	-0.15	0.19
Drepanidotaenia lateralis	-0.27	0.36
Aploparaxis sp.	-0.02	-0.22
Anomotaenia dominicanus	-0.19	0.33
Choanotaenia porosa	0.08	-0.11
Tetrabothrius cylindraceus	0.01	0.05
Diphyllobothrium sp.	-0.04	0.07
Nematodes		
Cosmocephalus obvelatus	-0.52[1]	0.44[1]
Capillaria sp.1	-0.36[1]	0.34[1]
Capillaria sp.2	-0.26	0.37[1]

Note: correlation coefficients with a superscript ([1]) are significant.

Table 11. Spearman Rank correlations between each of the helminth species and the first two components resulting from the principal components analysis on the covariance matrix of the log(x+1)-transformed abundance data from adult ring billed gulls collected at the four nesting colonies along the St. Lawrence River and Estuary.

	Principal component 1	Principal component 2
Percent of variation explained	41.5	12.2
Digeneans		
Diplostomum spathaceum ssp.	0.97[1]	-0.39[1]
Mesophorodiplostomum pricei	0.02	0.04
Cardiocephalus medioconiger	0.01	0.04
Cotylurus platycephalus	0.23	-0.19
Apophallus brevis	0.12	-0.45[1]
Echinostoma sp.	-0.20	0.18
Himasthala leptosoma	-0.01	-0.20
Stephanoprora denticulata	0.39[1]	-0.30
Maritreminoides sp.	0.32	-0.37[1]
Plagiorchis multiglandularis	0.02	-0.02
Cestodes		
Wardium stellorae	0.16	0.37[1]
W. cirrosa	-0.01	-0.54[1]
W. clavicirrus	0.17	-0.28
Wardium sp.1	0.00	0.78[1]
Wardium sp.2	-0.05	0.16
Wardium sp.3	-0.09	-0.22
Microsomacanthus charadrii	0.10	-0.15
M. ductilis	0.21	-0.16
Drepanidotaenia lateralis	-0.15	-0.34[1]
Aploparaxis sp.	-0.09	-0.22
Anomotaenia dominicanus	0.13	-0.09
Choanotaenia porosa	0.13	-0.19
Tetrabothrius cylindraceus	0.14	-0.10
Diphyllobothrium sp.	0.15	-0.06
Nematodes		
Cosmocephalus obvelatus	0.14	-0.53[1]
Capillaria sp.1	0.28	-0.38[1]
Capillaria sp.2	0.19	-0.32

Note: correlation coefficients with a superscript ([1]) are significant.

Table 12. Comparison of the helminth infracommunities in adult ring billed gulls collected at Montreal prior to, during and following the nesting season.

	April	June	August '94	August '95
No. examined	8	10	10	15
Total # species	14	15	15	14
Mean # species / bird (SD)	3.9 (2.0)	4.4 (2.3)	5.6 (1.7)	4.2 (1.6)
Range of species	1 - 6	2 - 8	3 - 8	1 - 7
Mean # worms / bird (SD)	27.5 (26.5)[1]	64.6 (63.8)	105.0 (62.2)[1]	131.3 (250.5)
Range of # worms	3 - 85	7 - 171	49 - 213	6 - 1002
Mean Brillouin's Index (SD)	0.26 (0.19)	0.33 (0.17)	0.45 (0.16)	0.29 (0.13)
Mean Eveness score (SD)	0.50 (0.37)	0.66 (0.25)	0.64 (0.14)	0.52 (0.25)

Note: Values with a superscript ([1]) are significantly different from each other.

Table 13. Comparison of the helminth component communities of adult ring billed gulls collected at Montreal prior to, during and following the nesting season.

	April	June	August '94	August '95
Total	220[1]	646	1050	1969
	100[2]	100	100	100
Digenea	27	288	683	1580
	12.3	44.6	65.0	80.2
Cestoda	170	358	356	386
	77.3	55.4	33.9	19.6
Nematoda	23	0	11	3
	10.4	0	1.0	0.2

1 - Number of worms in each taxon; 2 - Percent of total (%).

Table 14. The prevalence (% birds infected) of the helminth species recovered from adult ring billed gulls collected at Montreal prior to, during and following the nesting season.

Parasite	April	June	August '94	August '95
Digeneans				
***Diplostomum spathaceum* ssp.**	-	80	80	66.7
Mesophorodiplostomum pricei	-	30	50	6.7
Cardiocephalus medioconiger	-	10	-	-
Apophallus brevis	12.5	30	40	26.7
Echinostoma sp.	12.5	-	10	33.3
Stephanoprora denticulata	50	20	60	40
Plagiorchis multiglandularis	12.5	-	100	73.3
Cestodes				
Wardium stellorae	37.5	50	40	46.7
W. cirrosa	-	-	10	-
W. clavicirrus	-	-	10	-
Wardium sp.1	62.5	70	60	53.3
Wardium sp.2	12.5	20	-	6.7
Wardium sp.3	-	10	-	-
Microsomacanthus charadrii	-	20	-	6.7
M. ductilis	-	20	-	-
Drepanidotaenia lateralis	12.5	10	-	-
Aploparaxis sp.	12.5	10	-	-
Anomotaenia dominicanus	25	-	10	13.4
Choanotaenia porosa	25	40	30	26.7
Tetrabothrius cylindraceus	12.5	20	-	-
Nematodes				
Cosmocephalus obvelatus	37.5	-	30	6.7
***Capillaria* sp.1**	62.5	-	10	13.4
Capillaria sp.2	-	-	20	-

Note: Species names in **bold** indicate significant that differences exist between the four collections.

Table 15. The mean abundance (and standard deviation) of the helminth species recovered from adult ring billed gulls collected at Montreal prior to, during and following the nesting season.

Parasite	April	June	August '94	August '95
Digeneans				
***Diplostomum spathaceum* ssp.**	-[1,2]	24.0 (38.1)[1]	8.7 (9.8)[2]	5.5 (12.2)
Mesophorodiplostomum pricei	-	2.1 (5.6)	10.3 (19.7)	0.5 (1.8)
Cardiocephalus medioconiger	-	0.1 (0.3)	-	-
Apophallus brevis	0.1 (0.4)	2.0 (5.3)	11.3 (23.1)	2.9 (10.5)
Echinostoma sp.	0.2 (0.7)	-	0.4 (1.3)	21.3 (34.9)
Stephanoprora denticulata	2.9 (5.8)	0.6 (1.3)	7.6 (12.7)	8.3 (27.2)
Plagiorchis multiglandularis	0.1 (0.4)[1]	-[2,3]	30.0 (24.2)[1,2]	66.7 (204.9)[3]
Cestodes				
Wardium stellorae	11.8 (26.6)	13.0 (27.2)	2.8 (5.6)	12.4 (26.2)
W. cirrosa	-	-	2.8 (8.8)	-
W. clavicirrus	-	-	0.4 (1.3)	-
Wardium sp.1	5.5 (5.8)	10.5 (12.1)	28.4 (36.9)	10.2 (19.2)
Wardium sp.2	2.4 (6.7)	0.9 (2.0)	-	1.4 (5.4)
Wardium sp.3	-	0.3 (0.9)	-	-
Microsomacanthus charadrii	-	7.7 (17.4)	-	0.1 (0.5)
M. ductilis	-	1.9 (5.7)	-	-
Drepanidotaenia lateralis	0.1 (0.4)	0.2 (0.6)	-	-
Aploparaxis sp.	0.5 (1.4)	0.1 (0.3)	-	-
Anomotaenia dominicanus	0.5 (1.1)	-	0.8 (2.5)	0.3 (1.0)
Choanotaenia porosa	0.4 (0.7)	0.8 (1.2)	0.4 (0.7)	1.3 (2.2)
Tetrabothrius cylindraceus	0.1 (0.4)	0.4 (1.0)	-	-
Nematodes				
Cosmocephalus obvelatus	1.1 (2.4)	-	0.7 (1.2)	0.7 (0.2)
***Capillaria* sp.1**	1.8 (2.0)	-	0.1 (0.3)	0.1 (0.4)
Capillaria sp.2	-	-	0.3 (0.7)	-

Note: Species names in **bold** indicate that significant differences exist between the four collections. Cells within the same row that have the same superscript are significantly different from each other.

Table 16. Mean Jaccard's coefficients and mean percent similarity scores for the helminth communities in adult ring billed gulls collected at Montreal prior to, during and following the nesting period. These were calculated from all of the possible pairwise comparisons within and between collections.

Jaccard's Coeficients (S.D.)

	April	June	August '94	August '95
April	19.7 (22.3)	0.19 (0.18)	0.14 (0.13)	0.16 (0.15) / 0.16 (0.14)
June	20.1 (22.8)	27.2 (21.5)	0.24 (0.15)	0.22 (0.15) / 0.21 (0.15)
August '94	17.7 (22.2)	20.2 (19.6)	34.1 (22.2)	0.36 (0.16) / 0.32 (0.18)
August '95	15.4 (22.5)	19.2 (22.8)	22.5 (22.3)	23.8 (25.5) / 0.28 (0.17)

Mean Percent Similarity (S.D.)

Table 17. Spearman Rank correlations between each of the helminth species and the first three dimensions resulting from non-metric multidimensional scaling of the mean percent similarity scores of adult ring billed gulls collected at Montreal prior to, during and following the nesting season.

	Dimension 1	Dimension 2	Dimension 3
Percent of variance explained	20.8	13.3	9.7
Digeneans			
Diplostomum spathaceum ssp.	0.06	0.16	0.70[1]
Mesophorodiplostomum pricei	0.18	0.31[1]	0.40[1]
Cardiocephalus medioconiger	-0.19	-0.14	0.04
Apophallus brevis	0.01	0.22	0.25
Echinostoma sp.	-0.04	0.40[1]	0.03
Stephanoprora denticulata	-0.29	0.05	0.24
Plagiorchis multiglandularis	-0.13	0.56[1]	0.57[1]
Cestodes			
Wardium stellorae	-0.66[1]	-0.46[1]	0.18
W. cirrosa	0.15	0.23	-0.01
W. clavicirrus	0.15	0.23	-0.01
Wardium sp.1	0.66[1]	-0.04	0.13
Wardium sp.2	0.04	-0.09	-0.32[1]
Wardium sp.3	0.24	0.01	-0.10
Microsomacanthus charadrii	0.26	0.22	-0.20
M. ductilis	0.16	0.02	0.09
Drepanidotaenia lateralis	-0.32[1]	-0.01	-0.12
Aploparaxis sp.	-0.03	0.10	-0.22
Anomotaenia dominicanus	0.03	0.16	-0.08
Choanotaenia porosa	0.04	-0.03	-0.02
Tetrabothrius cylindraceus	-0.02	0.09	-0.04
Nematodes			
Cosmocephalus obvelatus	0.01	0.04	0.09
Capillaria sp.1	0.04	-0.35[1]	-0.25
Capillaria sp.2	0.12	0.06	0.19

Note: Correlation coefficients with a superscript ([1]) are significant.

Table 18. Spearman Rank correlations between each of the helminth species and the first two principal components resulting from principal components analysis of the presence or absence data from adult ring billed gulls collected at various times of the year at Montreal.

	Principal component 1	Principal component 2
Percent of variance explained	31.7	13.6
Digeneans		
Diplostomum spathaceum ssp.	0.05	0.19
Mesophorodiplostomum pricei	0.19	0.29
Cardiocephalus medioconiger	-0.19	-0.14
Apophallus brevis	0.03	0.23
Echinostoma sp.	-0.05	0.38[1]
Stephanoprora denticulata	-0.31[1]	-0.01
Plagiorchis multiglandularis	-0.16	0.47[1]
Cestodes		
Wardium stellorae	-0.62[1]	-0.41[1]
W. cirrosa	0.15	0.23
W. clavicirrus		
Wardium sp.1	0.72[1]	-0.09
Wardium sp.2	0.07	-0.08
Wardium sp.3		
Microsomacanthus charadrii	0.26	0.23
M. ductilis	0.16	0.02
Drepanidotaenia lateralis	-0.32[1]	-0.01
Aploparaxis sp.	0.02	0.10
Anomotaenia dominicanus	0.01	0.16
Choanotaenia porosa	0.08	0.04
Tetrabothrius cylindraceus	-0.02	0.01
Nematodes		
Cosmocephalus obvelatus	0.00	0.04
Capillaria sp.1	0.06	-0.34[1]
Capillaria sp.2	0.12	0.05

Note: Correlation coefficients with a superscript ([1]) are significant.

Table 19. Spearman Rank correlations between each of the helminth species and the first two principal components resulting from principal components analysis of covariance matrix of the log(x+1) transformed abundance data from adult ring billed gulls collected at Montreal prior to, during and following the nesting season.

	Principal component 1	Principal component 2
Percent of variance explained	38.9	14.4
Digeneans		
Diplostomum spathaceum ssp.	0.34[1]	0.05
Mesophorodiplostomum pricei	0.34[1]	0.05
Cardiocephalus medioconiger	0.01	-0.15
Apophallus brevis	0.19	-0.15
Echinostoma sp.	-0.08	-0.24
Stephanoprora denticulata	-0.11	-0.11
Plagiorchis multiglandularis	0.36[1]	-0.23
Cestodes		
Wardium stellorae	-0.07	0.09
W. cirrosa	0.20	0.01
W. clavicirrus	0.20	0.01
Wardium sp.1	0.06	-0.07
Wardium sp.2	0.00	0.38[1]
Wardium sp.3	0.10	0.24
Microsomacanthus charadrii	0.16	0.23
M. ductilis	0.09	0.35[1]
Drepanidotaenia lateralis	-0.08	0.04
Aploparaxis sp.	-0.02	0.32[1]
Anomotaenia dominicanus	-0.02	-0.17
Choanotaenia porosa	0.09	0.17
Tetrabothrius cylindraceus	0.00	0.41[1]
Nematodes		
Cosmocephalus obvelatus	-0.03	-0.28
Capillaria sp.1	-0.21	-0.24
Capillaria sp.2	0.28	-0.06

Note: Correlation coefficients with a superscript ([1]) are significant

Table 20. Comparison of the helminth infracommunities in juvenile ring billed gulls collected at Montreal.

	June (2 weeks)	June (4 weeks)	June (fledged)	August '94	August '95	November
No. examined	15	14	10	10	17	10
Total # species	2	9	10	12	15	5
Mean # species / bird (SD)	1.2 (0.4)[1,3]	2.7 (1.2)[5]	2.4 (1.2)	4.4 (2.0)[1,2]	3.8 (1.8)[3,4]	0.8 (0.9)[2,4,5]
Range of species	1 - 2	1 - 4	1 - 5	2 - 7	0 - 7	0 - 2
Mean # worms / bird (SD)	28.7 (19.5)	159.1 (141.3)[1]	126.0 (76.8)[2]	118.0 (208.6)[3]	44.5 (49.6)	7.7 (13.2)[1,2,3]
Range of # worms	6 - 70	6 - 527	20 - 225	6 - 700	0 - 177	0 - 38
Mean Brillouin's Index (SD)	0.01 (0.02)[1,2]	0.18 (0.14)[1,3]	0.10 (0.11)[4,5]	0.32 (0.15)[1,4,6]	0.32 (0.17)[2,3,5,7]	0.05 (0.08)[3,,6,7]
Mean Eveness score (SD)	0.04 (0.09)[1,2,3]	0.42 (0.31)[1]	0.26 (0.30)[4,5]	0.64 (0.25)[2,4,6]	0.63 (0.29)[3,5,7]	0.24 (0.42)[6,7]

Note: Values with the same superscript are significantly different from each other.

Table 21. Composition of the helminth component communities of juvenile ring billed gulls collected at Montreal.

	June (2 weeks)	June (4 weeks)	June (fledged)	August '94	August '95	November
Total	430[1]	2227	1260	1180	757	77
	100[2]	100	100	100	100	100
Digenea	425	1573	1246	222	463	71
	98.8	70.64	98.89	18.81	61.16	92.20
Cestoda	2	649	0	917	253	6
	0.5	29.14	0	77.71	33.42	7.80
Nematoda	3	5	14	41	41	0
	0.7	0.22	1.11	3.48	5.42	0

1 - Number of worms in each taxon; 2 - Percent of total (%)

Table 22. The prevalence (% birds infected) of the helminth species recovered from juvenile ring billed gulls collected at Montreal.

Parasite	June (2 weeks)	June (4 weeks)	June (fledged)	August 1994	August 1995	November
Digeneans						
D. spathaceum	-	-	-	80	52.94	20
M. pricei	-	-	20	20	17.65	-
C. .medioconiger	-	-	10	10	5.88	-
C. Platycephalus	-	-	20	-	-	-
A. brevis	-	7.14	10	40	23.53	10
Echinostoma sp.	-	-	-	-	11.76	-
H. leptosoma	-	-	-	-	5.88	-
S. denticulata	-	14.28	10	40	41.18	10
Maritreminoides sp.	-	-	10	-	-	-
P. multiglandularis	100	100	100	70	41.18	-
Cestodes						
W. stellorae	-	35.71	-	60	29.41	10
W. cirrosa	-	7.14	-	-	-	-
***Wardium* sp.1**	-	64.28	-	20	17.65	-
***Wardium* sp.2**	6.67	7.14	-	-	41.18	-
O. proteus	-	-	-	-	5.88	-
C. porosa	-	7.14	-	-	17.65	30
Nematodes						
C. obvelatus	13.33	28.57	40	50	52.94	-
Tetrameres sp.	-	-	-	10	-	-
Capillaria sp.1	-	-	10	10	23.53	-
***Capillaria* sp.2**	-	-	10	30	-	-

Note: Helminth names in **bold** show a significant difference between the collections.

Table 23. The mean abundance (and standard deviation) of the helminth species recovered from juvenile ring billed gulls collected at Montreal.

Parasite	June (2 weeks)	June (4 weeks)	June (fledged)	August 1994	August 1995	November
Digeneans						
D. spathaceum	-[1]	-[2]	-[3]	11.1 (16.8)[1,2,3]	16.8 (40.0)	2.7 (7.0)
M. pricei	-	-	2.9 (8.8)	0.3 (0.7)	1.5 (3.4)	-
C. medioconiger	-	-	0.6 (1.9)	0.1 (0.3)	0.4 (1.4)	-
C. platycephalus	-	-	0.4 (1.0)	-	-	-
A. brevis	-	0.6 (2.1)	0.2 (0.6)	4.7 (8.9)	0.4 (0.8)	0.6 (2.0)
Echinostoma sp.	-	-	-	-	1.7 (5.7)	-
H. leptosoma	-	-	-	-	0.1 (0.2)	-
S. denticulata	-	0.1 (0.4)	0.4 (1.3)	0.8 (1.3)	5.0 (11.0)	3.8 (12.0)
Maritreminoides sp.	-	-	0.4 (1.3)	-	-	-
P. multiglandularis	28.3 (19.1)[1,2]	111.6 (87.3)[3,4,5]	119.7 (80.9)[6,7,8]	5.2 (6.1)[3,6]	1.4 (3.0)[1,4,7]	-[2,5,8]
Cestodes						
W. stellorae	-	24.3 (78.4)	-	65.8 (162.4)[1]	6.7 (23.6)[1]	0.1 (0.3)
W. cirrosa	-	0.1 (0.3)	-	-	-	-
***Wardium* sp.1**	-[1]	21.6 (40.3)[1]	-	25.9 (58.3)	0.5 (1.1)	-
***Wardium* sp.2**	0.13 (0.5)	0.3 (1.1)	-	-	4.8 (8.2)	-
O. proteus	-	-	-	-	2.1 (8.5)	-
C. porosa	-	0.1 (0.3)	-	-	0.9 (2.2)	0.5 (0.8)
Nematodes						
C. obvelatus	0.2 (0.6)	0.4 (0.6)	0.9 (1.4)	2.5 (5.2)	2.1 (3.2)	-
Tetrameres sp.	-	-	-	0.2 (0.6)	-	-
Capillaria sp.1	-	-	0.1 (0.3)	1.0 (3.2)	0.4 (0.8)	-
***Capillaria* sp.2**	-	-	0.4 (1.3)	0.4 (0.7)	-	-

Note: Helminth names in **bold** show a significant difference between the collections. Cells within the same row that have the same superscript are significantly different.

Table 24. Mean Jaccard's coefficients and mean percent similarity scores for helminth communities in juvenile ring billed gulls collected at Montreal. These were calculated from all of the possible pairwise comparisons within and between collections.

Jaccard's coefficients

	June (2 weeks)	June (4 weeks)	June (fledged)	August '94	August '95	November
June (2 weeks)	0.82 (0.25)	0.46 (0.27)	0.51 (0.26)	0.20 (0.19)	0.13 (0.16)	0.00 (0.00)
June (4 weeks)	98.6 (2.2)	0.43 (0.19)	0.34 (0.19)	0.24 (0.17)	0.17 (0.16)	0.02 (0.07)
June (fledged)	77.7 (24.7)	68.9 (24.6)	0.38 (0.20)	0.22 (0.19)	0.15 (0.15)	0.00 (0.03)
August '94	89.9 (15.7)	73.1 (24.8)	82.6 (19.4)	0.30 (0.17)	0.23 (0.18)	0.06 (0.11)
August '95	17.2 (22.2)	21.7 (21.6)	17.7 (22.3)	23.7 (23.6)	0.20 (0.17)	0.05 (0.11)
November	8.6 (14.6)	11.1 (15.3)	9.6 (15.0)	17.8 (19.8)	12.2 (15.3)	0.4 (0.12)
	0.00 (0.0)	0.8 (4.0)	0.1 (0.5)	6.9 (16.2)	11.4 (19.3)	2.9 (12.0)

Mean percent similarity

Table 25. Spearman Rank correlations between each of the helminth species and the first two dimensions resulting from non-metric multidimensional scaling of the Jaccard coefficients of young of the year ring billed gulls collected at Montreal.

	Dimension 1	Dimension 2
Percent of variation explained	21.2	9.2
Digeneans		
Diplostomum spathaceum ssp.	-0.49[1]	-0.13
Mesophorodiplostomum pricei	-0.18	-0.26[1]
Cardiocephalus medioconiger	0.00	-0.05
Cotylurus platycephalus	0.17	0.23[1]
Apophallus brevis	-0.31[1]	-0.21
Echinostoma sp.	-0.17	-0.18
Himasthala leptosoma	-0.13	-0.18
Stephanoprora denticulata	-0.28[1]	0.10
Maritreminoides sp.	0.04	0.16
Plagiorchis multiglandularis	0.62[1]	-0.08
Cestodes		
Wardium stellorae	-0.36[1]	-0.03
W. cirrosa	-0.03	-0.02
Wardium sp.1	-0.20	-0.18
Wardium sp.2	-0.16	-0.13
Ophryocotyle proteus	-0.04	-0.17
Choanotaenia porosa	-0.36[1]	0.00
Nematodes		
Cosmocephalus obvelatus	-0.11	-0.61[1]
Tetrameres sp.	-0.04	-0.06
Capillaria sp.1	-0.26[1]	-0.38[1]
Capillaria sp.2	-0.18	0.05

Note: Correlation coefficients with a superscript ([1]) are significant.

Table 26. Spearman Rank correlations between each of the helminth species and the first two dimensions resulting from non-metric multidimensional scaling of the mean percent similarity scores of young of the year ring billed gulls collected at Montreal.

	Dimension 1	Dimension 2
Percent of variance explained	32.5	8.9
Digeneans		
Diplostomum spathaceum ssp.	-0.54[1]	0.56[1]
Mesophorodiplostomum pricei	-0.17	0.22
Cardiocephalus medioconiger	-0.12	0.20
Cotylurus platycephalus	0.20	0.05
Apophallus brevis	-0.30[1]	0.34[1]
Echinostoma sp.	-0.26[1]	0.01
Himasthala leptosoma	-0.17	0.14
Stephanoprora denticulata	-0.26[1]	0.51[1]
Maritreminoides sp.	0.08	0.04
Plagiorchis multiglandularis	0.78[1]	-0.20
Cestodes		
Wardium stellorae	-0.36[1]	-0.36[1]
W. cirrosa	0.04	-0.11
Wardium sp.1	-0.08	-0.02
Wardium sp.2	-0.32[1]	-0.15
Ophryocotyle proteus	-0.20	-0.14
Choanotaenia porosa	-0.34[1]	-0.04
Nematodes		
Cosmocephalus obvelatus	-0.25[1]	0.28[1]
Tetrameres sp.	-0.06	0.14
Capillaria sp.1	-0.18	0.06
Capillaria sp.2	-0.13	-0.03

Note: Correlation coefficients with a superscript ([1]) are significant

Table 27. Spearman Rank correlations between each of the helminth species and the first two principal components resulting from principal components analysis on the presence or absence data for young of the year ring billed gulls collected at Montreal.

	Principal component 1	Principal component 2
Percent of variance explained	43.8	12.2
Digeneans		
Diplostomum spathaceum ssp.	-0.02	-0.76[1]
Mesophorodiplostomum pricei	-0.11	-0.24[1]
Cardiocephalus medioconiger	-0.01	-0.19
Cotylurus platycephalus	-0.14	0.18
Apophallus brevis	0.13	-0.54[1]
Echinostoma sp.	-0.26[1]	-0.15
Himasthala leptosoma	-0.16	-0.16
Stephanoprora denticulata	-0.01	-0.42[1]
Maritreminoides sp.	-0.10	-0.05
Plagiorchis multiglandularis	0.75[1]	0.62[1]
Cestodes		
Wardium stellorae	0.18	-0.04
W. cirrosa	0.06	0.21
Wardium sp.1	0.41[1]	-0.01
Wardium sp.2	-0.24[1]	-0.04
Ophryocotyle proteus	-0.19	-0.09
Choanotaenia porosa	-0.25[1]	-0.25[1]
Nematodes		
Cosmocephalus obvelatus	0.39[1]	-0.54[1]
Tetrameres sp.	0.19	-0.18
Capillaria sp.1	-0.02	-0.28[1]
Capillaria sp.2	-0.13	-0.04

Note: Correlation coefficients with a superscript ([1]) are significant.

Table 28. Spearman Rank correlations between each of the helminth species and the first two principal components resulting from principal components analysis on the covariance matrix of the log(x+1)-transformed abundance data for young of the year ring billed gulls collected at Montreal.

	Principal component 1	Principal component 2
Percent of variance explained	52.9	14.4
Digeneans		
Diplostomum spathaceum ssp.	-0.38[1]	-0.43[1]
Mesophorodiplostomum pricei	0.02	0.00
Cardiocephalus medioconiger	0.05	-0.06
Cotylurus platycephalus	0.18	0.26[1]
Apophallus brevis	-0.05	-0.20
Echinostoma sp.	-0.18	-0.09
Himasthala leptosoma	-0.07	-0.05
Stephanoprora denticulata	-0.23	-0.36[1]
Maritreminoides sp.	0.09	0.16
Plagiorchis multiglandularis	0.74[1]	0.42[1]
Cestodes		
Wardium stellorae	-0.12	-0.18
W. cirrosa	-0.08	-0.06
Wardium sp.1	0.24[1]	-0.28[1]
Wardium sp.2	-0.33[1]	-0.35[1]
Ophryocotyle proteus	-0.10	-0.10
Choanotaenia porosa	-0.16	-0.14
Nematodes		
Cosmocephalus obvelatus	0.02	-0.03
Tetrameres sp.	-0.02	-0.20
Capillaria sp.1	-0.05	-0.02
Capillaria sp.2	-0.12	-0.11

Note: Correlation coefficients with a superscript ([1]) are significant.

Table 29. Comparison of the helminth infracommunities in adult and juvenile ring billed gulls collected at Montreal in August.

	Adults		Juveniles	
	1994	1995	1994	1995
No. examined	10	15	10	17
Total # species	15	14	12	15
Mean # species / bird (SD)	5.6 (1.7)	4.2 (1.6)	4.4 (2.0)	3.8 (1.8)
Range of species	3 - 8	1 - 7	2 - 7	0 - 7
Mean # worms / bird (SD)	105.0 (62.2)	131.3 (250.5)	118.0 (208.6)	44.5 (49.6)
Range of # worms	49 - 213	6 - 1002	6 - 700	0 - 177
Mean Brillouin's Index (SD)	0.45 (0.16)	0.29 (0.13)	0.32 (0.15)	0.32 (0.17)
Mean Eveness score (SD)	0.64 (0.14)	0.52 (0.25)	0.64 (0.25)	0.63 (0.29)

Table 30. Comparison of the helminth component communities of adult and juvenile ring billed gulls collected at Montreal in August.

	Adults		Juveniles	
	1994	1995	1994	1995
Total	1050[1]	1969	1180	757
	100[2]	100	100	100
Digenea	683	1580	222	463
	65.0	80.2	18.81	61.16
Cestoda	356	386	917	253
	33.9	19.6	77.71	33.42
Nematoda	11	3	41	41
	1.0	0.2	3.48	5.42

1 - Number of worms in each taxon; 2 - Percent of total (%).

Table 31. The prevalence (% birds infected) of the helminth species recovered from adult and juvenile ring billed gulls collected at Montreal in August.

Parasite	Adults		Juveniles	
	August '94	August '95	August '94	August '95
Digeneans				
Diplostomum spathaceum ssp.	80	66.7	80	52.94
Mesophorodiplostomum pricei	50	6.7	20	17.65
Cardiocephalus medioconiger	-	-	10	5.88
Apophallus brevis	40	26.7	40	23.53
Echinostoma sp.	10	33.3	-	11.76
Himasthala leptosoma	-	-	-	5.88
Stephanoprora denticulata	60	40	40	41.18
Plagiorchis multiglandularis	100	73.3	70	41.18
Cestodes				
Wardium stellorae	40	46.7	60	29.41
W. cirrosa	10	-	-	-
W. clavicirrus	10	-	-	-
***Wardium* sp.1**	60	53.3	20	17.65
***Wardium* sp.2**	-	6.7	-	41.18
Microsomacanthus charadrii	-	6.7	-	-
Anomotaenia dominicanus	10	13.4	-	-
Ophryocotyle proteus	-	-	-	5.88
Choanotaenia porosa	30	26.7	-	17.65
Nematodes				
Cosmocephalus obvelatus	30	6.7	50	52.94
Tetrameres sp.	-	-	10	-
Capillaria sp.1	10	13.4	10	23.53
***Capilaria* sp.2**	20	-	30	-

Note: Helminth names in **bold** show a significant difference between collections.

Table 32. The mean abundance (and standard deviation) of the helminth species recovered from adult and juvenile ring billed gulls collected at Montreal in August.

Parasite	Adults		Juveniles	
	1994	1995	1994	1995
Digeneans				
Diplostomum spathaceum ssp.	8.7 (9.8)	5.5 (12.2)	11.1 (16.8)	16.8 (40.0)
Mesophorodiplostomum pricei	10.3 (19.7)	0.5 (1.8)	0.3 (0.7)	1.5 (3.4)
Cardiocephalus medioconiger	-	-	0.1 (0.3)	0.4 (1.4)
Apophallus brevis	11.3 (23.1)	2.9 (10.5)	4.7 (8.9)	0.4 (0.8)
Echinostoma sp.	0.4 (1.3)	21.3 (34.9)	-	1.7 (5.7)
Himasthala leptosoma	-	-	-	0.1 (0.2)
Stephanoprora denticulata	7.6 (12.7)	8.3 (27.2)	0.8 (1.3)	5.0 (11.0)
Plagiorchis multiglandularis	30.0 (24.2)[1,2]	66.7 (204.9)[1]	5.2 (6.1)	1.4 (3.0)[2]
Cestodes				
Wardium stellorae	2.8 (5.6)	12.4 (26.2)	65.8 (162.4)	6.7 (23.6)
W. cirrosa	2.8 (8.8)	-	-	-
W. clavicirrus	0.4 (1.3)	-	-	-
***Wardium* sp.1**	28.4 (36.9)	10.2 (19.2)	25.9 (58.3)	0.5 (1.1)
***Wardium* sp.2**	-	1.4 (5.4)	-	4.8 (8.2)
Microsomacanthus charadrii	-	0.1 (0.5)	-	-
Anomotaenia dominicanus	0.8 (2.5)	0.3 (1.0)	-	-
Ophryocotyle proteus	-	-	-	2.1 (8.5)
Choanotaenia porosa	0.4 (0.7)	1.3 (2.2)	-	0.9 (2.2)
Nematodes				
Cosmocephalus obvelatus	0.7 (1.2)	0.7 (0.2)	2.5 (5.2)	2.1 (3.2)
Tetrameres sp.	-	-	0.2 (0.6)	-
Capillaria sp.1	0.1 (0.3)	0.1 (0.4)	1.0 (3.2)	0.4 (0.8)
***Capillaria* sp.2**	0.3 (0.7)	-	0.4 (0.7)	-

Note: Helminth names in **bold** show a significant difference between collections. Cells within the same row that have the same superscript are significantly different from each other.

Table 33. Mean Jaccard's coefficients and mean percent similarity scores for the helminth communities in adult and juvenile ring billed gulls collected at Montreal in August. These were calculated from all of the possible pairwise comparisons within and between collections.

Jaccard's Coeficients (S.D.)

	Adults		Juveniles	
	1994	1995	1994	1995
Adults 1994	0.36 (0.16) 34.1 (22.2)	0.32 (0.18)	0.32 (0.18)	
Adults 1995	22.5 (22.3)	0.28 (0.17) 23.8 (25.5)		0.20 (0.17)
Juveniles 1994	23.6 (19.5)		0.30 (0.17) 23.7 (23.6)	0.23 (0.18)
Juveniles 1995		12.2 (15.3)	17.8 (19.8)	0.20 (0.17) 12.2 (15.3)

Mean Percent Similarity (S.D.)

Table 34. Spearman Rank correlations between each of the helminth species and the first three dimensions resulting from non-metric multidimensional scaling of the mean percent similarity scores of juvenile and adult gulls collected at Montreal in August 1994 and 1995.

	Dimension 1	Dimension 2	Dimension 3
Percent variance explained	15.2	11.2	9.6
Digeneans			
Diplostomum spathaceum ssp.	0.60[1]	0.44[1]	-0.21
Mesophorodiplostomum pricei	0.05	0.48[1]	-0.02
Cardiocephalus medioconiger	-0.02	0.24	-0.11
Apophallus brevis	0.26	0.29[1]	0.06
Echinostoma sp.	0.16	-0.37[1]	0.32[1]
Himasthala leptosoma	0.09	0.20	-0.14
Stephanoprora denticulata	0.28[1]	0.16	0.21
Plagiorchis multiglandularis	0.24	0.14	0.31[1]
Cestodes			
Wardium stellorae	-0.51[1]	-0.34[1]	-0.51[1]
W. cirrosa	-0.21	0.24	0.08
W. clavicirrus	-0.21	0.24	0.08
Wardium sp.1	0.65[1]	-0.29[1]	-0.14
Wardium sp.2	-0.40[1]	-0.05	0.03
Microsomacanthus charadrii	0.02	-0.22	0.18
Anomotaenia dominicanus	0.02	0.08	0.10
Ophryocotyle proteus	-0.23	-0.09	-0.02
Choanotaenia porosa	0.12	-0.10	0.00
Nematodes			
Cosmocephalus obvelatus	-0.05	0.47[1]	0.04
Tetrameres sp.	0.05	0.18	0.01
Capillaria sp.1	-0.03	0.12	-0.23
Capillaria sp.2	0.18	-0.04	-0.28[1]

Note: Correlation coefficients with a superscript ([1]) are significant.

Table 35. Spearman Rank correlations between each of the helminth species and the first two principal components resulting from principal components analysis of the presence or absence data of juvenile and adult gulls collected at Montreal in August 1994 and 1995.

	Principal component 1	Principal component 2
Percent of variance explained	35.8	12.0
Digeneans		
Diplostomum spathaceum ssp.	0.57[1]	0.62[1]
Mesophorodiplostomum pricei	-0.01	0.26
Cardiocephalus medioconiger	0.02	0.12
Apophallus brevis	0.32[1]	0.53[1]
Echinostoma sp.	0.07	0.06
Himasthala leptosoma	-0.19	0.19
Stephanoprora denticulata	0.47[1]	0.08
Plagiorchis multiglandularis	0.63[1]	-0.25
Cestodes		
Wardium stellorae	0.15	-0.78[1]
W. cirrosa	-0.21	-0.08
W. clavicirrus	-0.21	-0.08
Wardium sp.1	0.35[1]	0.24[1]
Wardium sp.2	-0.42[1]	-0.08
Microsomacanthus charadrii	-0.17	-0.19
Anomotaenia dominicanus	-0.10	0.03
Ophryocotyle proteus	-0.20	-0.16
Choanotaenia porosa	-0.16	0.09
Nematodes		
Cosmocephalus obvelatus	-0.5	0.48[1]
Tetrameres sp.	0.06	0.14
Capillaria sp.1	-0.22	0.14
Capillaria sp.2	-0.04	-0.06

Note: Correlation coefficients with a superscript ([1]) are significant.

Table 36. Spearman Rank correlations between each of the helminth species and the first two principal components resulting from principal components analysis of the covariance matrix of the log(x+1)-transformed abundance data of juvenile and adult gulls collected at Montreal in August 1994 and 1995.

	Principal component 1	Principal component 2
Percent of variance explained	37.6	14.3
Digeneans		
Diplostomum spathaceum ssp.	0.72[1]	0.48[1]
Mesophorodiplostomum pricei	0.33[1]	0.43[1]
Cardiocephalus medioconiger	0.01	0.08
Apophallus brevis	0.36[1]	0.36
Echinostoma sp.	0.00	0.23
Himasthala leptosoma	0.04	0.22
Stephanoprora denticulata	0.37[1]	0.18
Plagiorchis multiglandularis	0.72[1]	0.22
Cestodes		
Wardium stellorae	-0.06	-0.86[1]
W. cirrosa	-0.15	0.17
W. clavicirrus	-0.15	0.17
Wardium sp.1	0.61[1]	0.08
Wardium sp.2	-0.40[1]	-0.19
Microsomacanthus charadrii	-0.13	-0.03
Anomotaenia dominicanus	0.06	0.23
Ophryocotyle proteus	-0.23	-0.18
Choanotaenia porosa	-0.02	0.12
Nematodes		
Cosmocephalus obvelatus	0.10	0.23
Tetrameres sp.	0.17	0.23
Capillaria sp.1	-0.12	0.09
Capillaria sp.2	0.12	-0.08

Note: Correlation coefficients with a superscript ([1]) are significant.

Figure 1: Number of common, intermediate and rare species in adult ring billed gulls collected at four nesting colonies along the St. Lawrence River and Estuary.

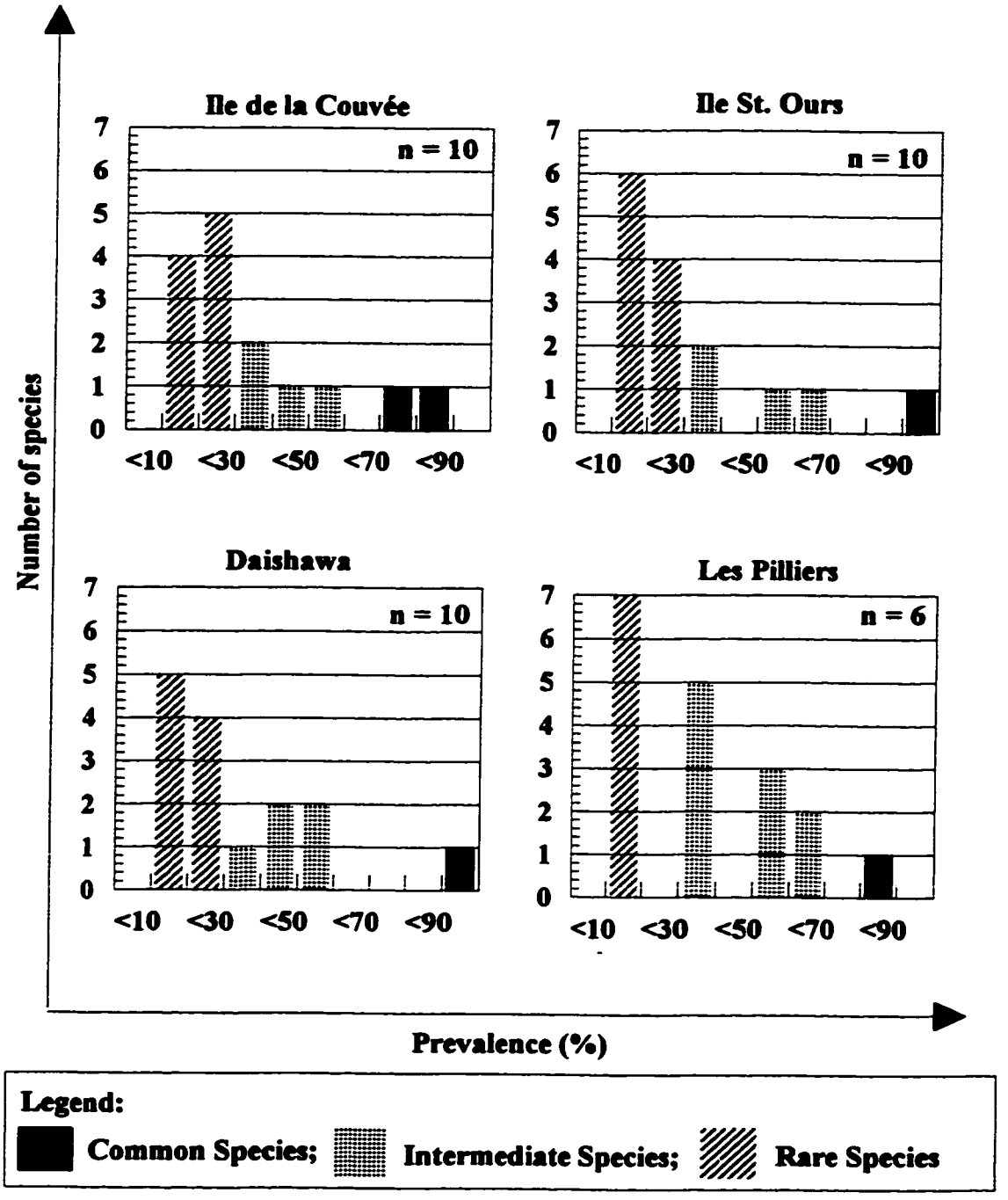
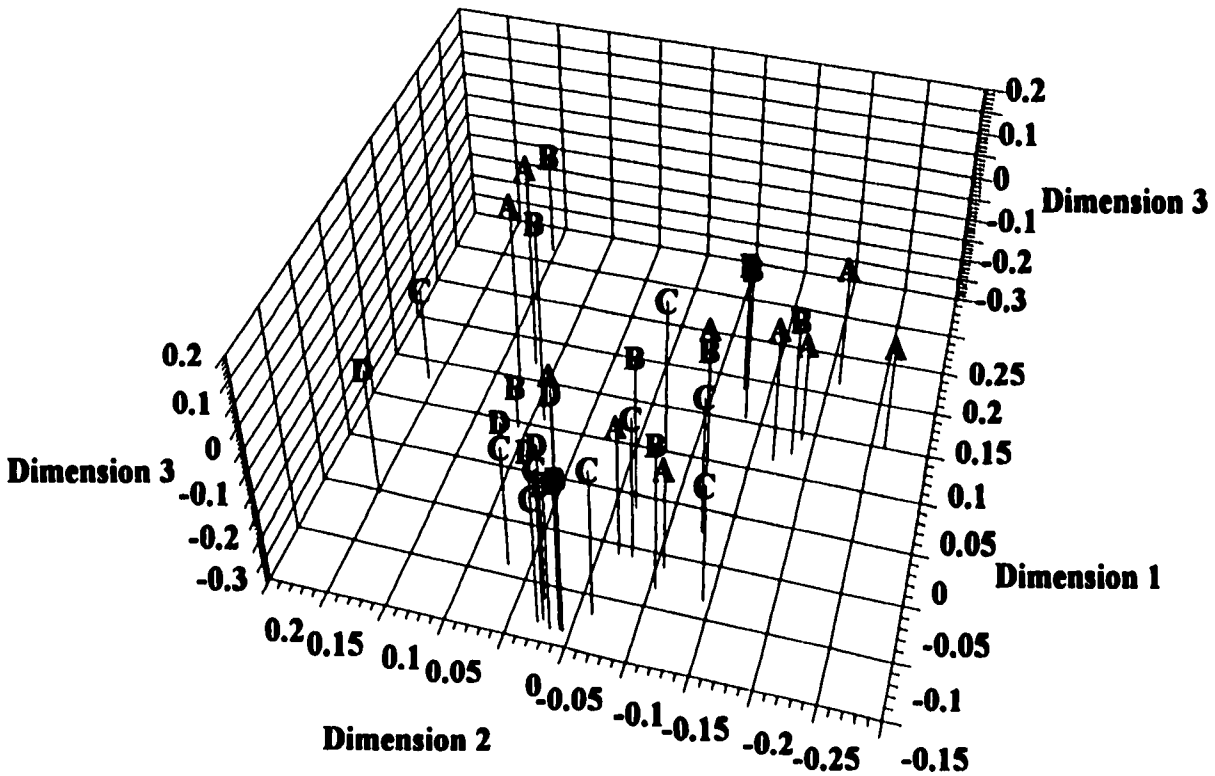


Figure 2: Plot of the first three dimensions derived from the non metric multidimensional scaling technique applied to the mean percent similarity scores for collections of adult ring billed gulls made at four nesting colonies along the St. Lawrence River and Estuary.



Legend:
A: Ile de la Couvée B: Ile St. Ours C: Daishawa D: Les Pilliers

Figure 3: Plot of the first two principal components resulting from the principal components analysis on the presence and absence of helminths recovered from ring billed gulls collected at four nesting colonies along the St. Lawrence River and Estuary.

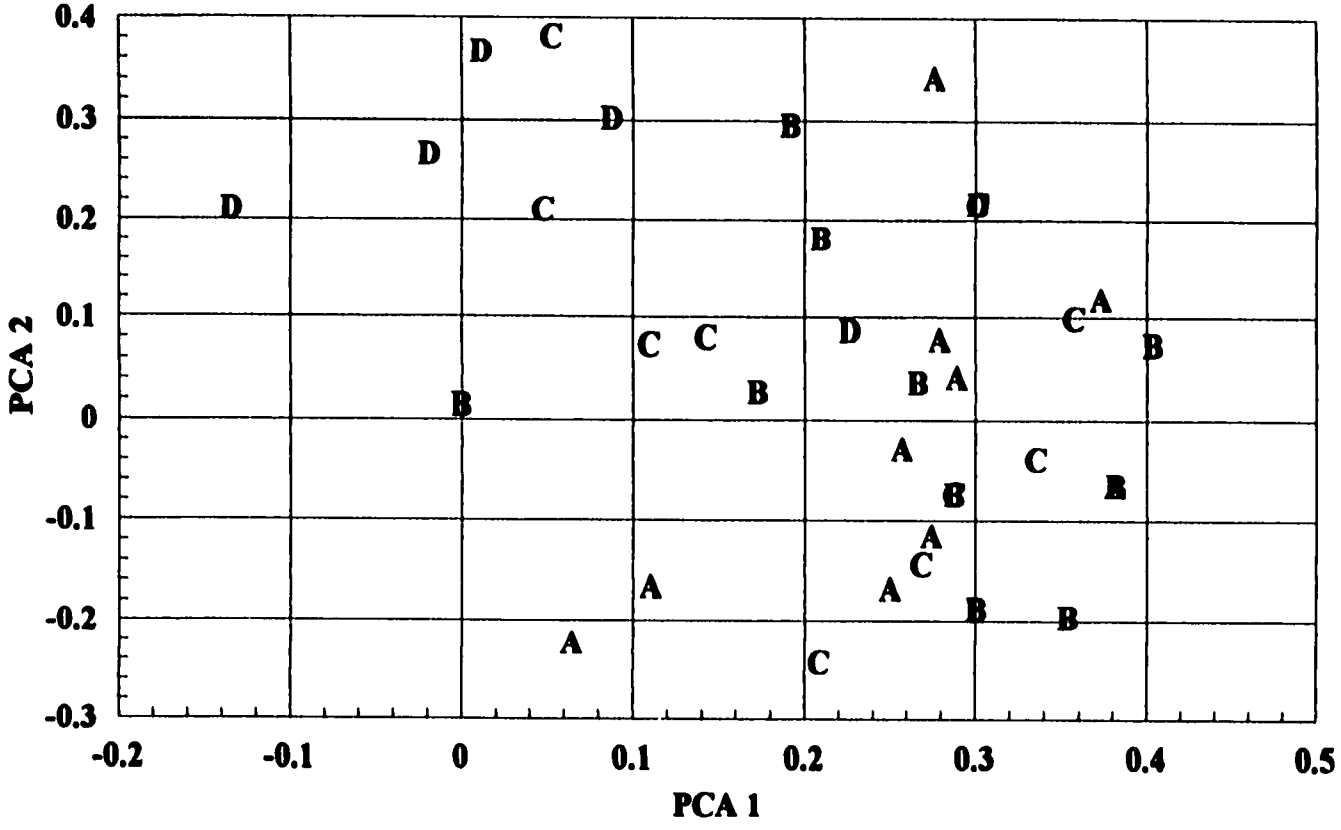


Figure 4: Plot of the first two principal components resulting from the principal components analysis on the log(x + 1) - transformed abundance data for adult ring billed gulls collected at four nesting colonies along the St. Lawrence River and Estuary.

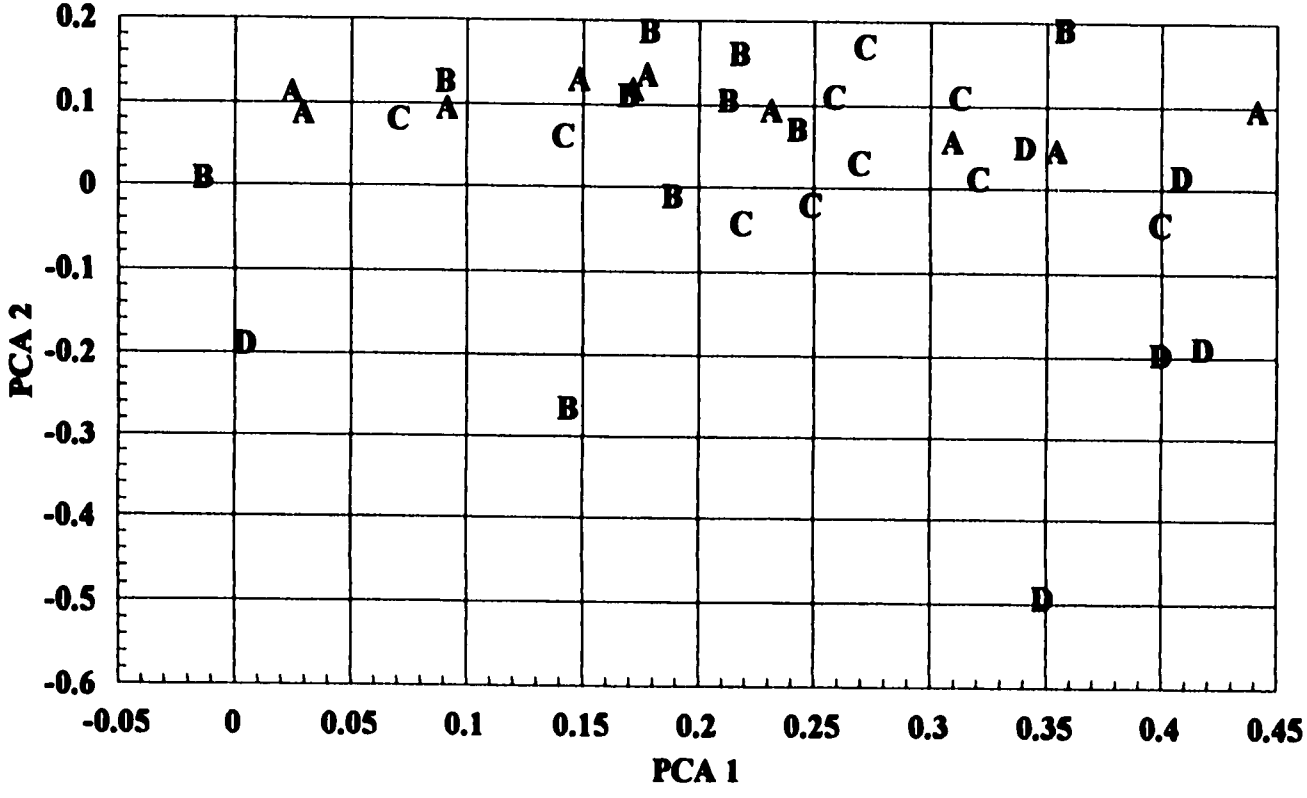
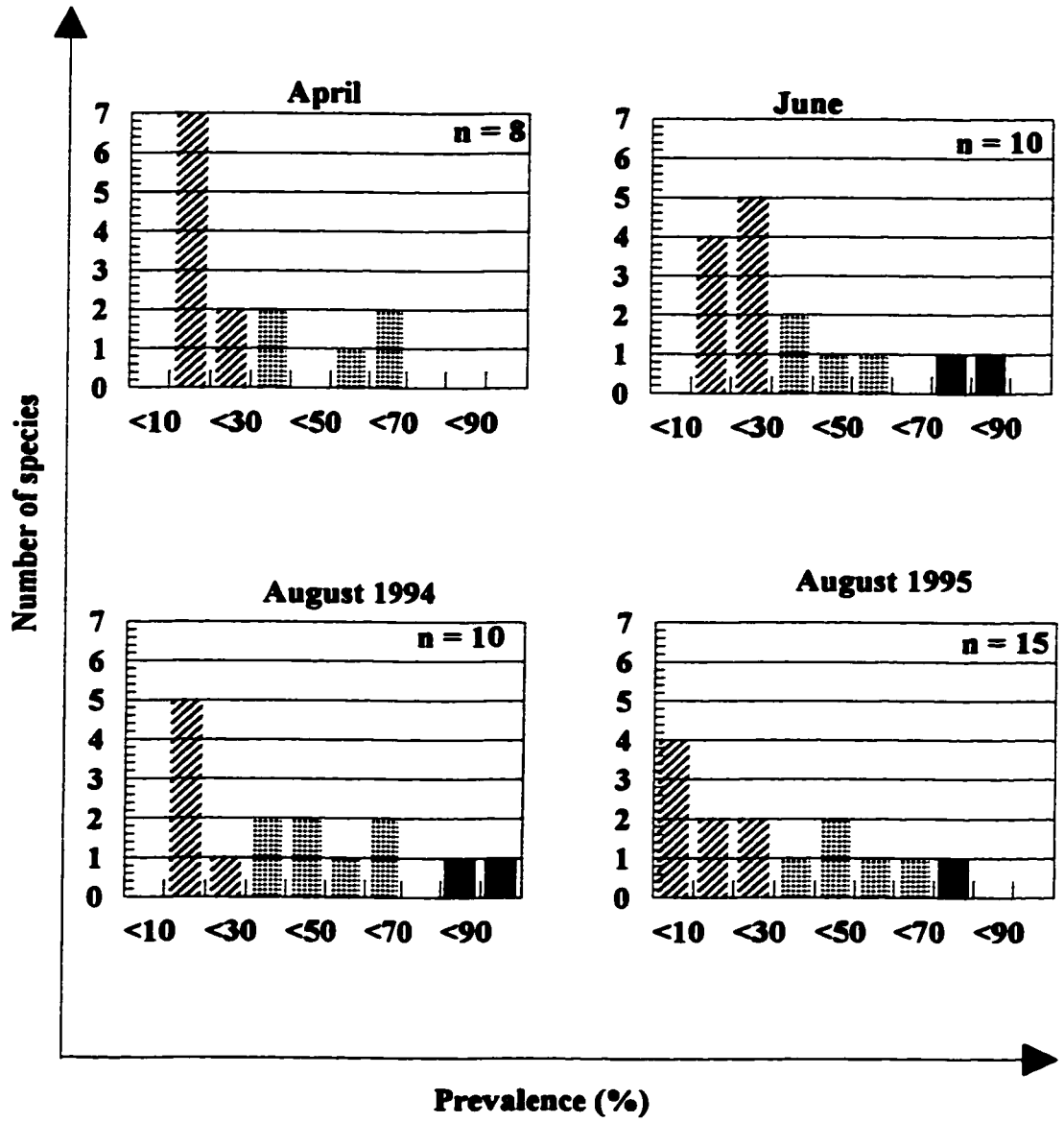


Figure 5: Number of common, intermediate, and rare species in adult ring billed gulls collected at Montreal prior to, during and following the nesting season.



Legend:

Common Species; Intermediate Species; Rare Species

Figure 6: First three dimensions resulting from subjecting the mean percent similarity scores derived from the mean percent similarity of four collections of adult ring billed gulls made at Montreal prior to, during and following the nesting season.

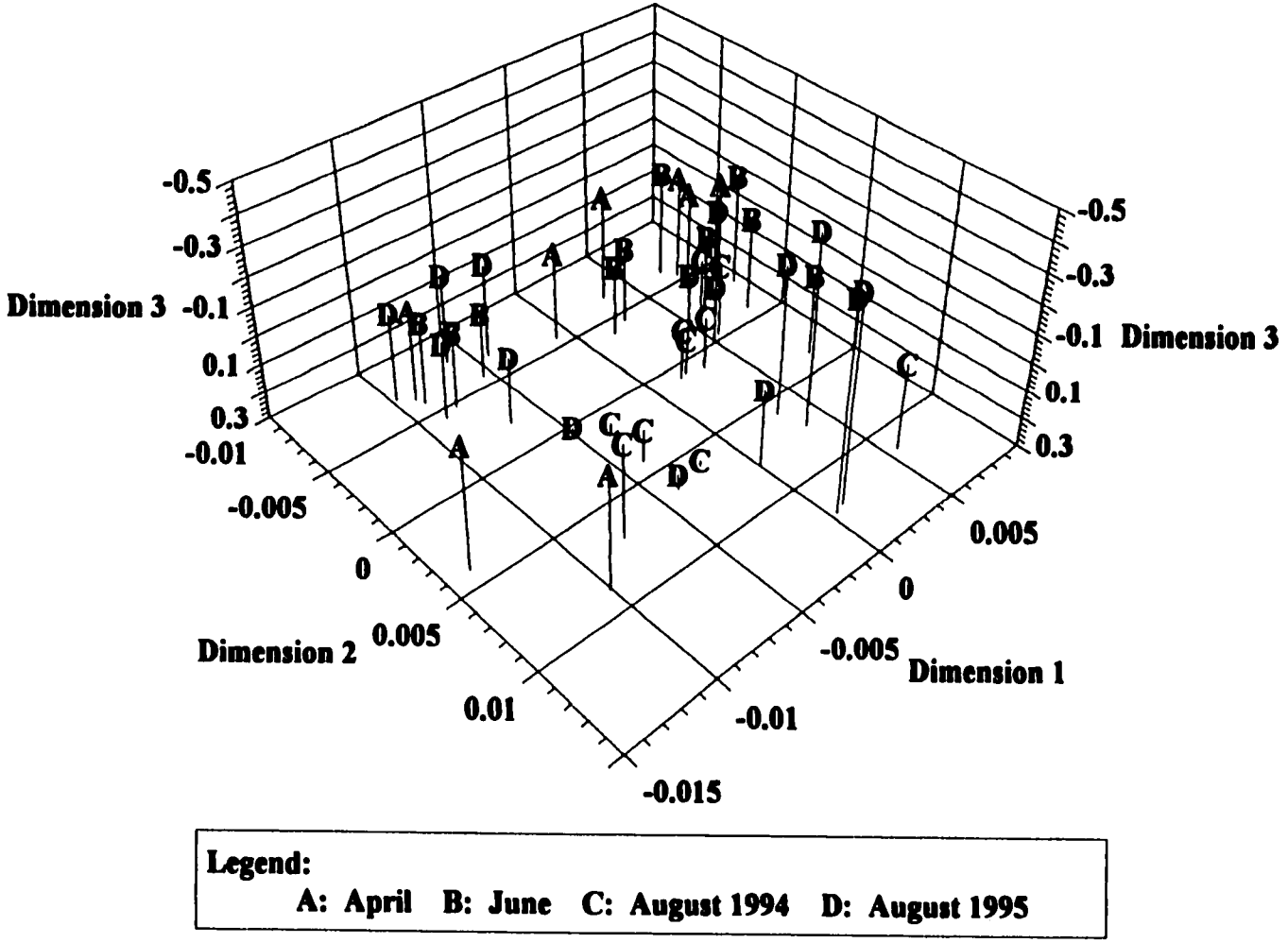


Figure 7: The first two principal components resulting from the principal components analysis of the presence or absence data for the helminths recovered from adult ring billed gulls collected at Montreal prior to, during and following the nesting season.

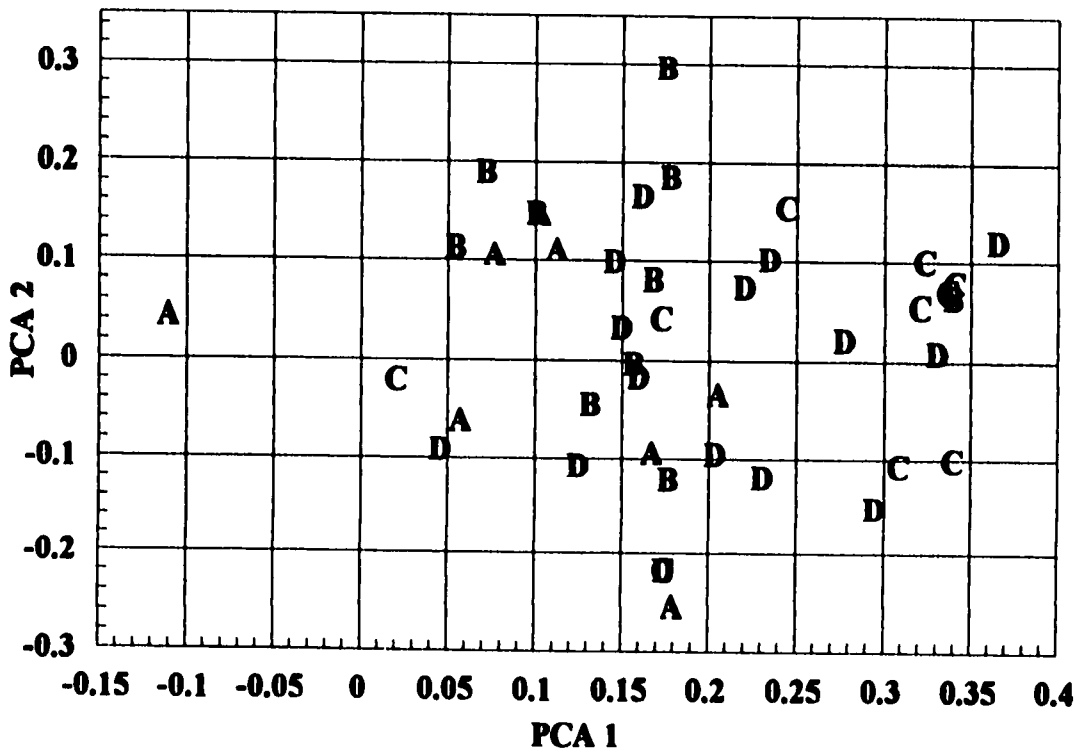


Figure 8: The first two principal components resulting from the principal components analysis of the log(x + 1) - transformed abundance data for the helminths recovered from adult ring billed gulls collected at Montreal prior to, during and following the nesting season.

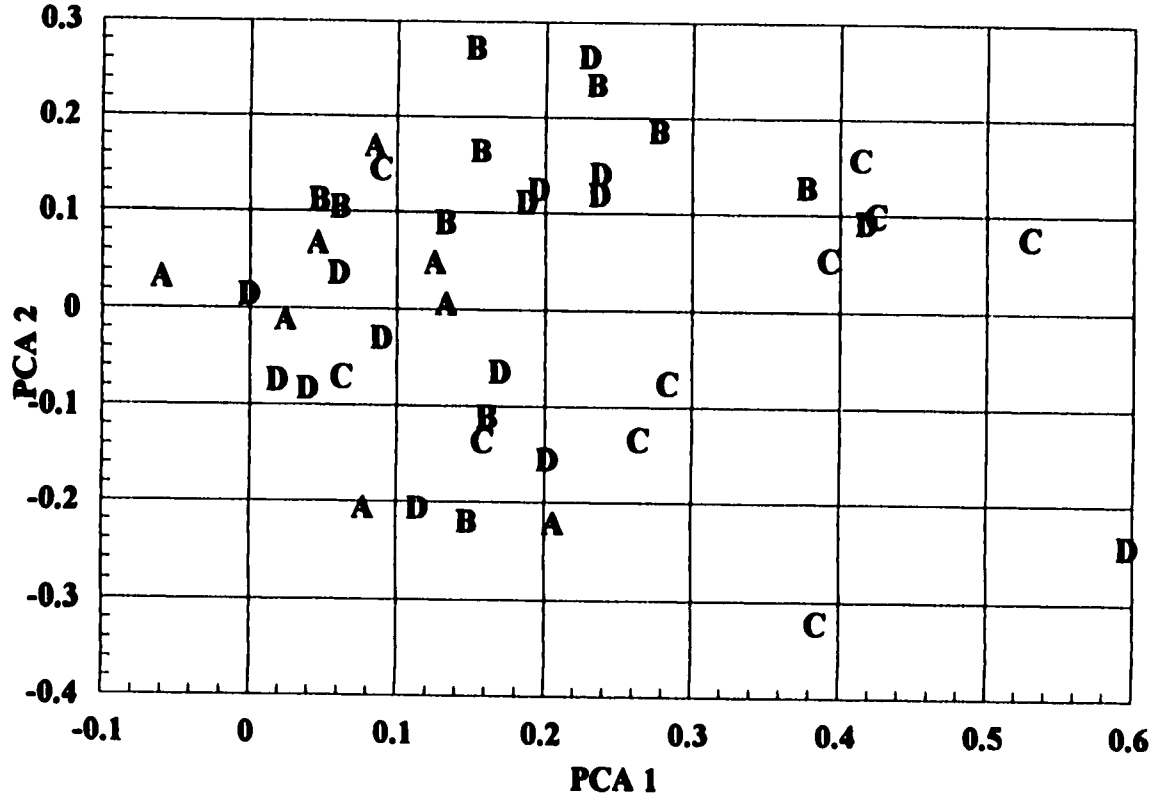


Figure 9: Number of common, intermediate and rare species in juvenile ring billed gulls made throughout the year at Montreal.

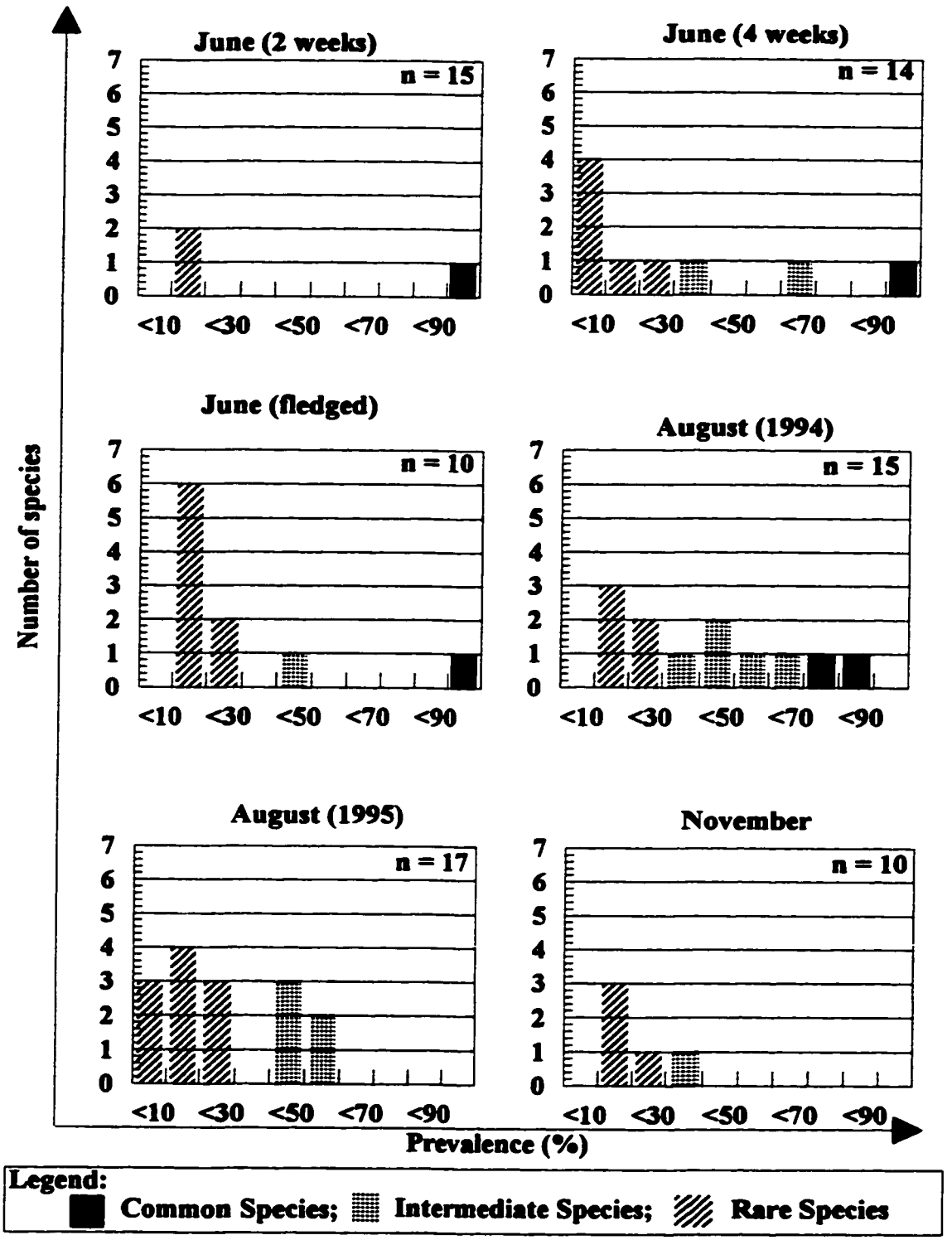


Figure 10: First two dimensions resulting from the multidimensional scaling of the Jaccard coefficient scores obtained from collections of juvenile ring billed gulls made throughout the year at Montreal.

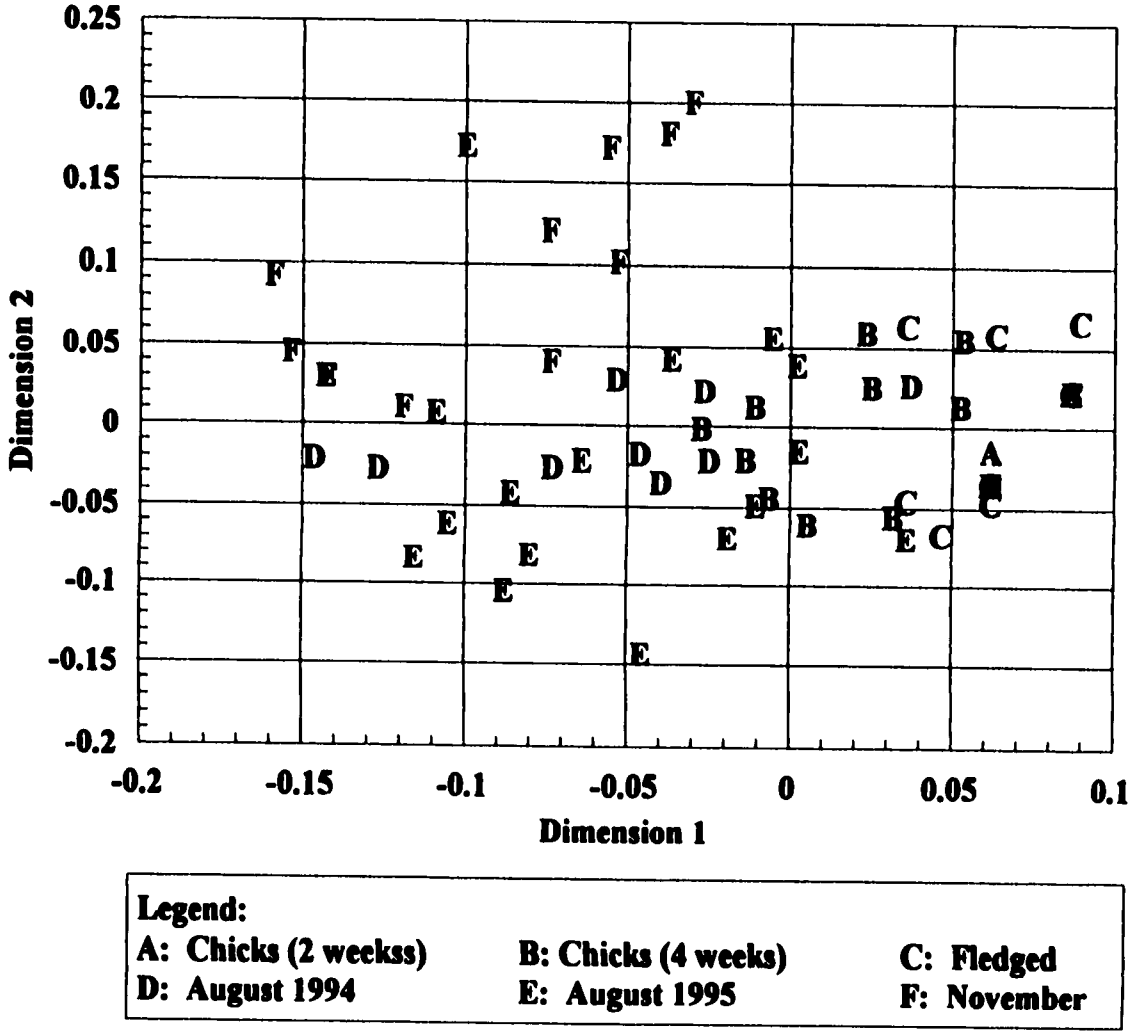
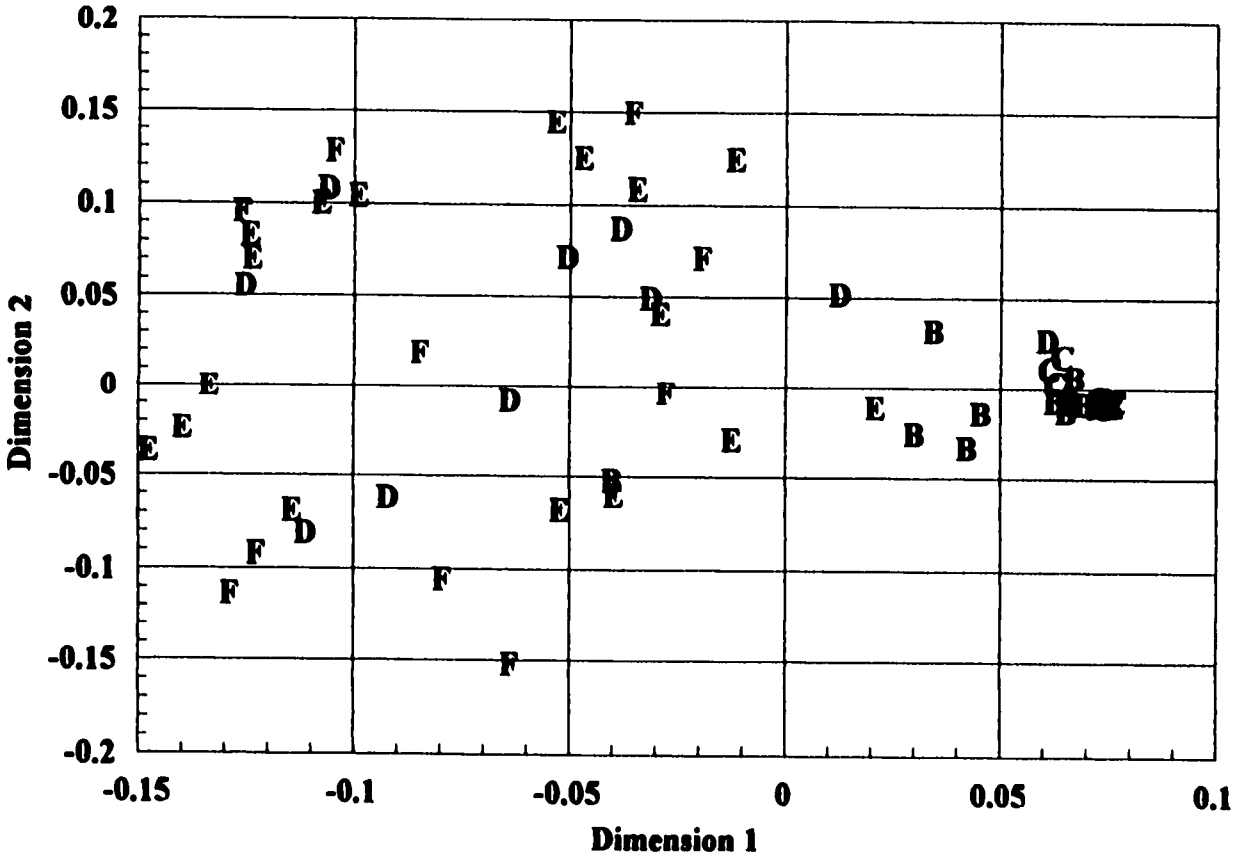


Figure 11: First two dimensions resulting from the multidimensional scaling of the mean percent similarity scores derived from collections of juvenile ring billed gulls made throughout the year at Montreal.



Legend:

A: Chicks (2 weeks)	B: Chicks (4weeks)	C: Fledged
D: August 1994	E: August 1995	F: November

Figure 12: The first two principal components resulting from principal components analysis of the presence or absence data for the helminths recovered from juvenile ring billed gulls collected throughout the year at Montreal.

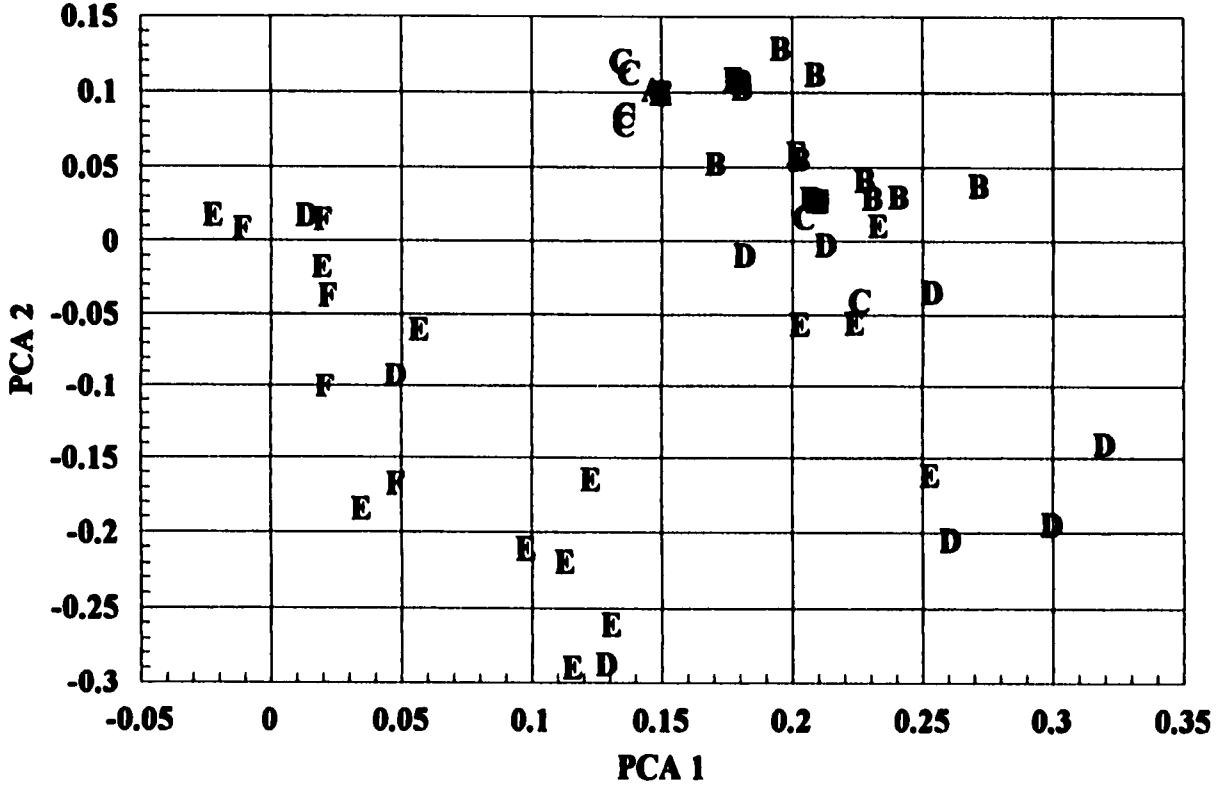


Figure 13: The first two principal components resulting from the principal components analysis of the log(x + 1) - transformed abundance data for the helminths recovered from juvenile ring billed gulls collected throughout the year at Montreal.

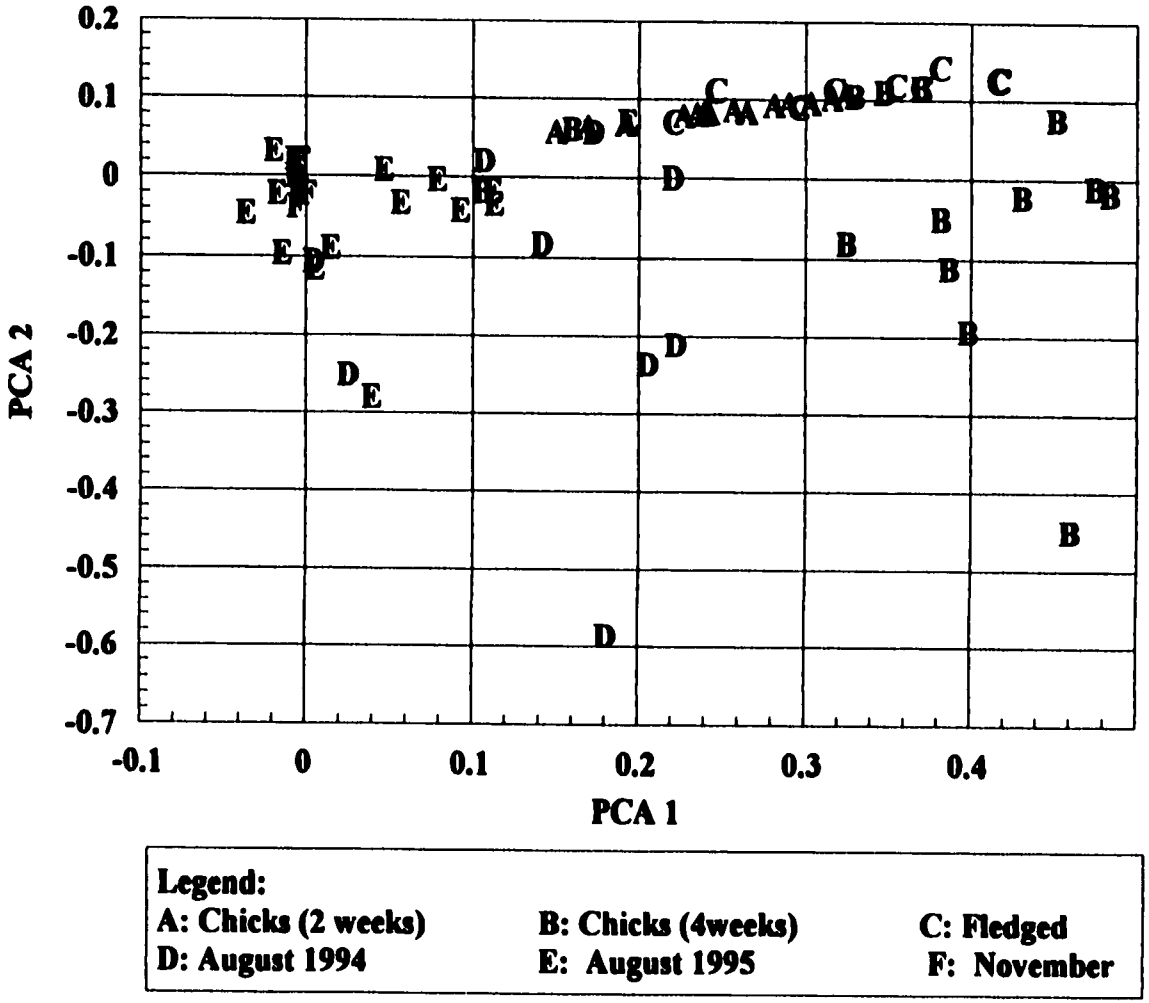


Figure 14: Number of common, intermediate, and rare species in adult and juvenile ring billed gulls collected at Montreal in August of two consecutive years.

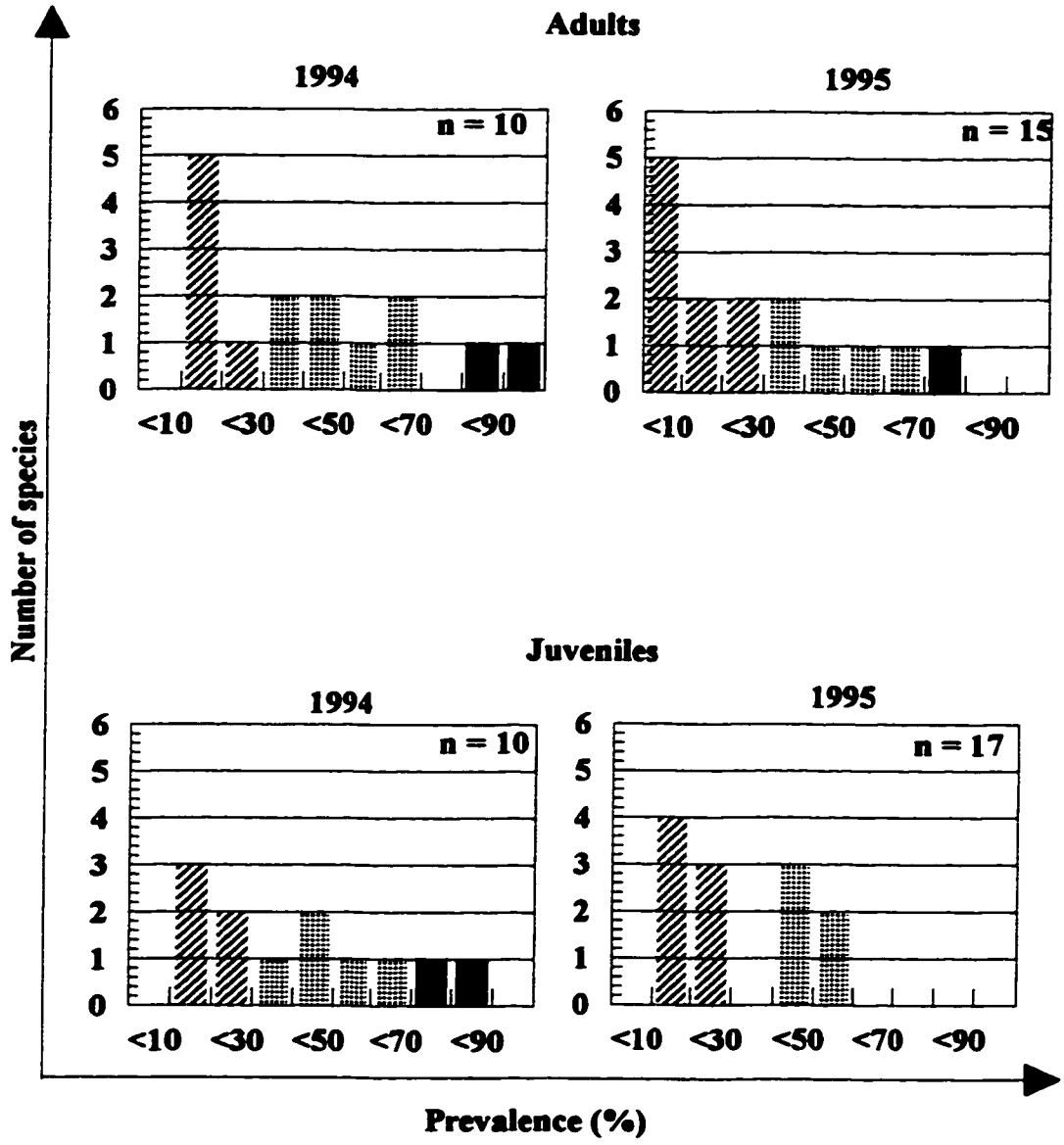
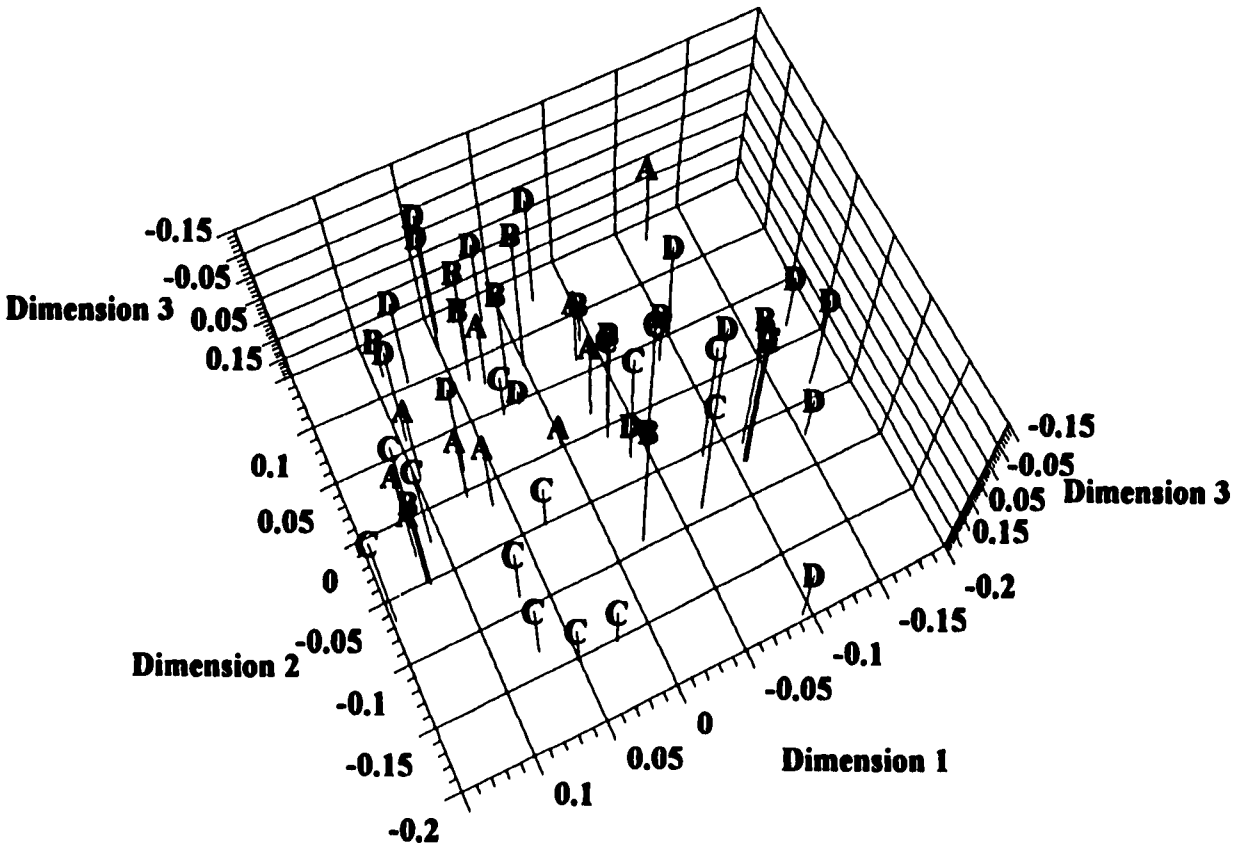


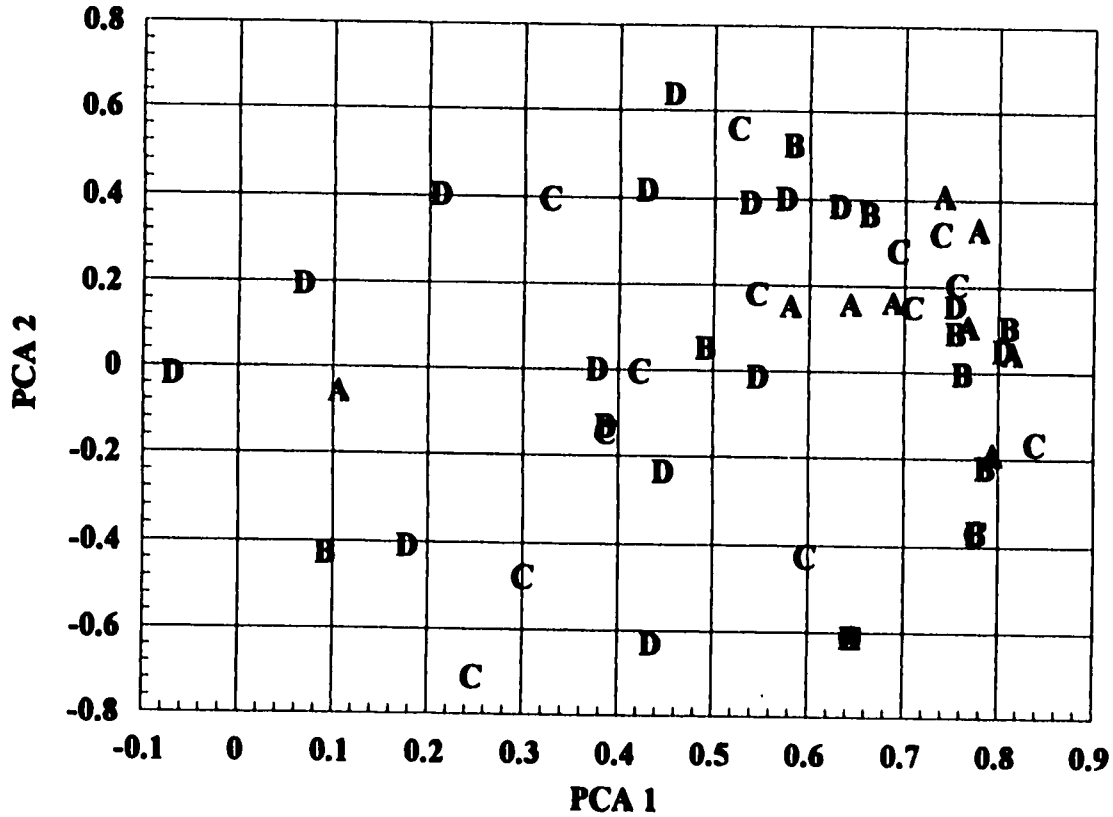
Figure 15: First three dimensions resulting from the multidimensional scaling of the mean percent similarity scores derived from collections of adult and juvenile ring billed gulls made at Montreal in August in two consecutive years.



Legend:

A: Adults 1994 B: Juveniles 1994 C: Adults 1995 D: Juveniles 1995

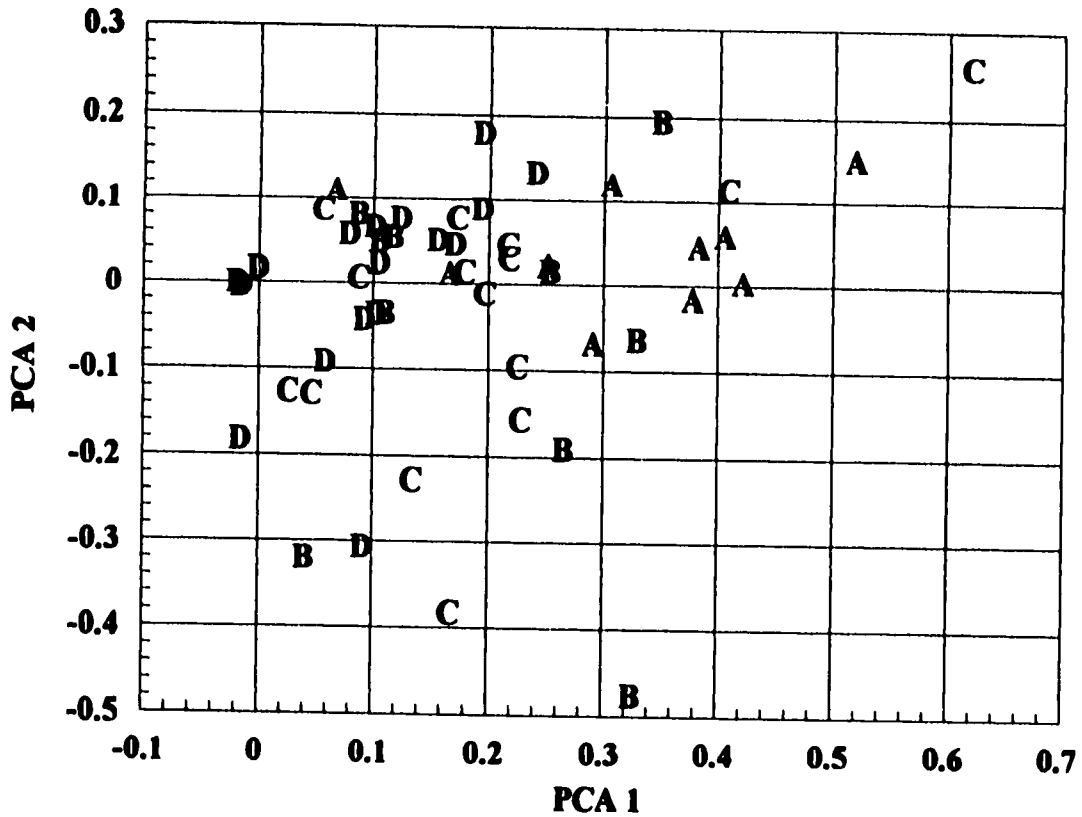
Figure 16: The first two principal components resulting from principal components analysis of the presence or absence data for the helminths recovered from adult and juvenile ring billed gulls collected at Montreal in August in two consecutive years.



Legend:

A: Audlts 1994 B: Juveniles 1994 C: Adults 1995 D: Juveniles 1995

Figure 17: The first two principal components resulting from principal components analysis of the log(x + 1) - transformed abundance data for the helminths recovered from adult and juvenile ring billed gulls collected at Montreal in August in two consecutive years.



Legend:

A: Audlts 1994 B: Juveniles 1994 C: Adults 1995 D: Juveniles 1995

APPENDIX 1

This macro was designed to calculate the analysis of similarity on a list of rank similarities. It was written in Microsoft Excel version 7.0. Three sheets must be present in the workbook. One sheet should be called 'Pivot', one should be called 'Sheet1' and the last should be a 'module' sheet (to hold the macro code).

Sheet1 should contain a list of rank similarities. Column 'A' should be a list of the type of comparison that the value in column 'B' pertains to; 'W' for within collection comparison and 'B' for between collection comparisons.

The 'Pivot' sheet should have a pivot table in cells 'A1' to 'C3'. The columns of this table must be the type of comparison (column 'A' in Sheet1), and the data should be the average rank (the average rank of the rank similarities (Column 'B' in sheet1) within a type ('W' or 'B')).

Cell 'E1' should have a label of 'N(N-1)/2'. Cell 'E2' should have that value (where N is the total number of samples used to generate the rank similarities). Column 'F' receives the list of R values, and column 'G' receives a list of integers showing which iteration each R was calculated from. Cell 'H2' receives an integer representing the number of times that the calculated R has been larger than, or equal to, the original R. Cell 'I2' receives an integer showing the total number of iterations and cell 'J2' receives the probability of getting the original R value given the frequency distribution created by the iterative technique on the data.

```
' RCALC Macro
' Macro created by Michael Levy to calculate analysis of similarity

Sub RCALC()
   HOWOFTEN = 1000 'change to change the number of iterations done

   'Copy original data
   Sheets("Sheet1").Select
   Range("A1").Select
   Selection.End(xlDown).Select
   Selection.Offset(0, 1).Activate
   Range("A1", ActiveCell).Select
   Selection.Copy
   Range("E2").Select
   ActiveSheet.Paste
   Range("E1").Value = "Copy of Original Data"

   'This section does the initial R calculation
   Sheets("Pivot").Select
   Range("F2").Select
   ActiveCell.Formula = "=((C3 - B3) / E2) / 2"
   Selection.Copy
   Selection.PasteSpecial Paste:=xlValues, Operation:=xlNone, _
      SkipBlanks:=False, Transpose:=False

   'Hold the calculated R
   R = Abs(Range("F2").Value)

   'Hold The number of times that other R's are >= R (Set to 1 for callculated)
   Bigger = 1

   'Hold Number of iterations
   Iter = 1
   Range("G2").Select
   ActiveCell.Value = Iter

   '-------------------------------------------------
   Do While Iter < HOWOFTEN

      'Select cells to assign random numbers for shuffle
      Sheets("Sheet1").Activate
      Range("B2").Select
      Selection.End(xlDown).Select
      Selection.Offset(0, 1).Activate
      Range("C2", ActiveCell).Select
```

```
        Selection.Formula = "=RAND()"

        'Do shuffle by sorting according to random numbers
          Range("B2").Select
        Selection.End(xlDown).Select
        Range("C2", ActiveCell).Select
       Selection.Sort Key1:=Range("C2"), Order1:=xlAscending, Header:= _
          xlGuess, OrderCustom:=1, MatchCase:=False, Orientation:= _
          xlTopToBottom

        'Refresh the Pivot table
         Sheets("Pivot").Select
        ActiveSheet.PivotTables("PivotTable1").RefreshTable

        'Calculate new R and place in right cell
        Range("F2").Select
        Selection.Offset(Iter, 0).Activate
        ActiveCell.Formula = "=((C3 - B3) / E2) / 2"
        Selection.Copy
        Selection.PasteSpecial Paste:=xlValues, Operation:=xlNone, _
           SkipBlanks:=False, Transpose:=False
       Rtmp = Abs(ActiveCell.Value)

       'Test if Rtmp is >= R, If yes then increment Bigger
       If R <= Rtmp Then Bigger = Bigger + 1

       'Increment Iter
       Iter = Iter + 1
       Selection.Offset(0, 1).Activate
       ActiveCell.Value = Iter
   Loop

   'Clean up
   Sheets("Sheet1").Select
   Range("C2").Select
   Selection.End(xlDown).Select
   Range("C2", ActiveCell).Select
   Selection.Clear
   Range("A1").Activate
   Sheets("Pivot").Select
   Range("H2").Value = Bigger
   Range("I2").Value = Iter
   Range("F2").Select
End Sub
```