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Development of metazoan parasite communities in the American eel, *Anguilla rostrata* : Patterns, Processes and Applicability as Biological Tags.

by

Duane Edward Barker

Submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Biology

at

Dalhousie University
Halifax, Nova Scotia
September, 1997

DALHOUSIE UNIVERSITY

FACULTY OF GRADUATE STUDIES

The undersigned hereby certify that they have read and recommend to the Faculty of Graduate Studies for acceptance a thesis entitled "Development of metazoan parasite communities in the American eel, *Anguilla rostrata*: Patterns, Processes and Applicability as Biological Tags"

by Duane Edward Barker

in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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Dedication

A dedication should be adressed to someone who played an integral role in the completion of an ultimate goal. With this in mind, I would like to dedicate this thesis to three people whom I feel were most responsible for me being able to reach my goal.

First, I would like to dedicate this work to my parents, Mr. R. Barker and Mrs. M. Barker. Thank you for letting me 'indulge' myself in the mystery of fishes, beginning with trout fishing as a child, then sculpin and flounder fishing from the wharf in my hometown. You continually supported every interest of mine, culminating with my interest in fish biology as a university student. I would not have accomplished such a goal were it not for your inspiration, patience and support.This thesis is dedicated to you.

Next, I would also like to dedicate this work to my 'mentor' during my university years at Memorial University, Dr. R.A. Khan. You introduced me to the fascinating world of parasites and the many possibilities of parasitological research. In addition, you continually demonstrated the rewards of diligence and perserverence. Thank you for believing in a 'young kid' back in 1987. This thesis is also dedicated to you.

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Abstract

American eels, *Anguilla rostrata*, were collected (via electrofisher and trap pots) from May to October, during 1995 and 1996, from 8 sample sites within a watershed (of varying pH and flow regime) in southwestern Nova Scotia. Aspects of eel biology and their metazoan parasites were examined to study: (i) the influence of host biology and season on the distribution of parasite fauna; (ii) the spatiotemporal dynamics of parasite component communities within the catchment; (iii) applicability of using several parasites as 'biological tags' (indicators) of eel riverine dispersal and (iv) developmental processes influencing both infra- and component community structure. During their first two years in freshwater, eels (6 to 10 cm) are free of metazoan parasites and disperse widely throughout the watershed. In their third year in freshwater, eels (10 to 13 cm) commence localized residency and begin to acquire metazoan parasites. Results of a two-year mark-recapture study demonstrated that 'yellow' eels (> 16 cm) are site specific with restricted home ranges. Eleven species of parasites were found within the watershed, six of which were host-specific to eels, while 5 were generalists (found as adults in a variey of fish species). Species richness and size of the parasite population of the intestinal helminth infracommunity increased with eel length, but for the majority of eels (~ 95%), the richness did not exceed 4 species. The majority of intestinal helminth infracommunities were dominated by eel specialists. The helminth community composition appeared to be most influenced by eel diet. Site to site variation among the intestinal helminth component communities was maintained by localized eel residency. Helminth component communities at sites of low pH (~ 4.3-5.2) were characterized by low species richness, low diversity and high dominance while opposite patterns were observed at sites of high pH (~ 5.5-6.8). The patterns observed among intestinal helminth component communities and pH parallelled those of free-living benthic macroinvertebrate assemblages at the same sites. Correspondence ordination further emphasized the linkage between parasite abundance and macroinvertebrate 'source' hosts with respect to pH. Consistency of annual patterns and predictability was attributed to the high proportion of specialists - thus implying the existence of a strong phylogenetic component in helminth community structure. From July to October, the seaward downstream migration of sexually maturing 'silver' eels could be plotted using changes in component community structure along the watershed. Parasites whose occurrence (and abundance) was influenced either by pH, stream flow or eel size, have good potential to be used as biological tags - indicators of eel riverine dispersal or habitat pH. It was concluded that ontogenetic (ultimate processes) influences (e.g. host biology, diet selectivity) were most important, as structuring processes, at the infracommunity level; but local habitat (proximate processes) was the most influential structuring process at the component community level. Furthermore, both processes (local and regional) were not mutually exclusive and it appeared phylogeny set the template (potential parasite species richness) but local ecological factors determined composition and abundance.

List of Abbreviations and Symbols Used

CA - Correspondence Analysis

CCR- Component Community Richness

CPUE - Catch per Unit Effort

DFO - Department of Fisheries and Oceans

H' - Shannon Index of Diversity

HSI - Hepatosomatic Index

ICR - Infracommunity Richness

J' - Pielou's Index of Evenness

N2 - Hill's Number of Diversity

S - Species Richness

VSI - Visceralosomatic Index

λ - Simpson Index of Dominance

Acknowledgements

Several people provided invaluble assistance throughout the duration of this thesis. First, I would like to thank my supervisor, Dr. D.K. Cone, who continuously provided time, advice, knowledge, supplies, laboratory facilities and the extended use of his electrofisher - I hope it still functions effectively. Second, I would like to thank Ms. T. Tizzard, for sampling assistance and more importantly, patience encouragement and reliability - you were always there for me. Third, I would like to thank Mr. J. Melendy for sampling and photographic assistance - and a great sense of humour. Fourth, a special thanks to Mr. P. Baltzar (and his loyal companion, Gunner) for sampling assistance in autumn 1994 and for the use of his eel pots. Fifth, I would like to thank several members of the Halifax Regional Fisheries Laboratory for their advice and cooperation in providing me with supplemental data on water chemistry (Mr. D. Ashfield), eel densities (Mr. P. Zamora), eel ageing (Mr. B. Jessop) and macroinvertebrate assemblages (Dr. N. Watson). Sixth, I would like to thank Dr. L. Vasseur of St. Mary's University, for her assistance (and 'magic touch') with correspondence analysis and CANOCO™ software. Finally, I wish to thank my thesis committe members (Dr. E. Angelopoulos, Dr. R. Doyle, Dr. J. Hutchings) for their time, advice and editorial comments.

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1. INTRODUCTION

1.1 Metazoan Parasite Communities - 'Structuring' Hypotheses

With the recent expansion in studies of parasitic helminth community ecology, interest has been focused on developing hypotheses of processes structuring intestinal helminth communities in vertebrate hosts. Previous studies of metazoan parasite communities among fishes have resulted in a variety of hypotheses to explain how such communities are structured (if they are structured). The work of Wisniewski (1958), Chubb (1963; 1970) and Leong and Holmes (1981) suggest intestinal helminth component communities of freshwater fishes are determined largely by the numerically dominant fish host present, which is often related to trophic status of a lake. Esch (1971) expanded the concept of numerically dominant host to conclude in oligotrophic lakes, parasite component communities of fishes were largely composed of **autogenic** species (parasites that complete their entire life cycle in freshwater), whereas in eutrophic lakes, the component communities of fishes were largely composed of **allogenic** species (parasites that mature in terrestrial hosts, e.g. birds, mammals). Others have noted the importance of regional factors (host phylogeny, biogeographical colonization events) as determinant processes of parasite communities in fishes (Halvorsen, 1971; Wootten, 1973; Esch *et al.*; 1988; Hartvigson and Halvorsen, 1993). Some hypotheses have their origins in free-living theory. Kennedy (1978) applied MacArthur and Wilson's (1963) 'island size' theory to explain patterns in helminth communities among populations of brown trout, *Salmo trutta*, in several British Lakes. The island size theory has also been applied at the infracommunity level, whereby host size was equivalent to island size, thus predicting larger hosts to have

richer and more diverse parasite communities (Bell and Burt, 1991). The application of Hanski's (1982) *core - satellite* model (derived from free-living theory) to parasite communities has been attempted (Hartvigsen and Halvorsen, 1993). One prediction of Hanski's (1982) model is that locally abundant species should be regionally widespread. Finally, the importance of local abiotic conditions (pH, lake depth, water chemistry) as a determinant process structuring the helminth communities of fishes has also been addressed (Marcogliese and Cone 1991; Cone *et al.* 1993; Marcogliese and Cone 1996).

The preceding hypotheses are not mutually exclusiv. Arguments that favour one hypothesis can equally support another. For example, the numerically dominant host of a lake could be related to trophic status and/or abiotic conditions, which are all 'ultimately' related to past biogeographic events. The hypotheses often reflect various viewpoints of different authors or the scale of the study. Basically, the hypotheses argue whether local ecology (**proximate** influence) is more important than phylogenetic history (**ultimate** influence) as a determinant process of parasite community structure. The validity of many of the preceding studies can be questioned because of a lack of long-term data and an evaluation of the parasite community as being characterized as a 'static', as opposed to 'dynamic' entity. Hypotheses have often been constructed based on mere 'snapshots' of parasite communities in fishes without any consideration for the influence of factors such as host biology (age, behaviour) and seasonality of the individual parasite life cycles.

The only comprehensive, long-term studies on helminth communities of fishes have been the result of work using the European eel, *Anguilla anguilla*. Among freshwater fishes, parasite infracommunities generally have been described as being 'species poor' and

isolationist in nature (Kennedy, 1990). Helminth infracommunities of European eels from Britain have been described as 'stochastic assemblages', with little potential for competitive interaction and were characterized by demonstrating low predictability (Kennedy, 1990, 1993). These communities were comprised largely of generalist parasites, and local ecological conditions promoting transmission were primarily responsible for determining infracommunity structure. Helminth component communities of these same eels, were also characterized by low diversity, low predictability and high variability (Kennedy, 1990). These communities were mostly dominated by generalists, whose presence was presumed to be a consequence of stochastic colonization events and whose abundance was related to favourable local conditions for transmission (Kennedy, 1990).

Studies on parasite communities of the American eel, *Anguilla rostrata*, a sister species to the European eel, are few, and no detailed studies exist. Marcogliese and Cone (1993) reported 6 species of host-specific parasites co-occurring in *A. anguilla* and *A. rostrata*. Cone *et al.* (1993) reported higher richness and diversity among metazoan parasite communities of American eels from an artificially limed portion of a watershed (pH 6.0-7.0) than among those from a naturally acidic portion of the same watershed (pH 4.4-5.5). This same trend within one watershed was reflected in regional patterns of eel parasite component communities across the province of Nova Scotia (Marcogliese and Cone, 1996). Although not explicitly cited in these papers, their work demonstrated two distinct differences between parasite communities in American and European eels, despite sharing several common parasite species: (i) consistency of patterns among parasite component communities of *A. rostata* over three years, thus possibility for predictability

and (ii) the parasite component communities of *A. rostata* were dominated by specialists, not generalists. It is these differences between parasite communities of *A. rostata* and *A. anguilla*, combined with a lack of any comprehensive study of metazoan parasites of *A. rostata*, which prompted this study.

1.2 Objectives

The present study was undertaken with several objectives. First, to assess the influence of host biology (age, diet, mobility) and season on the richness and composition of intestinal helminth infra- and component communities. Second, to determine if the parasite component communities display spatiotemporal variation in diversity and structure along a watershed. (If such heterogeneity exists, how is it maintained ?) Third, to determine the applicability of using several parasites as 'biological tags' (indicators of water quality and eel riverine dispersal). Finally, to attempt to identify the primary determinant processes (proximate vs. ultimate) influencing patterns among intestinal helminth infra- and component communities of American eel populations living within a watershed - an issue that has never been properly addressed in the literature.

1.3 Host Species

The American eel, *Anguilla rostrata*, was used in this study for several reasons. First, it is considered an 'old' species in an evolutionary context, with records dating back to the late Pleistocene (Cavender, 1986, cited in Marcogliese and Cone, 1993). Theoretically, sufficient time should have passed for coevolution of parasite and host.

Second, they have a catadromous life history. Sexually mature adults ('silver eels') will migrate in September and October from freshwater catchments to the Sargasso Sea to spawn then presumably die (Tesch, 1977). Upon hatching, the leptocephalus larvae will 'drift' in the Gulf Stream for about one year and then settle into bays and estuaries in April and May along the Atlantic Coast, where the larvae metamorphose into 'glass eels', resembling the adult body form, but being transparent (Tesch, 1977). In June and July, the glass eels acquire pigmentation when entering freshwater; and, as elvers, begin 'upstream' dispersion throughout watersheds. No marine metazoan parasites are brought into the freshwater system as these elvers are considered 'parasite-free' (Crane and Eversole, 1980; Field and Eversole, 1982). All metazoan parasites are acquired during the 'yellow eel' phase in freshwater.

Third, eels are among the most abundant freshwater fish in Nova Scotia, showing a widespread distribution (Jessop, 1987) that does not seem to be affected by regional differences in pH (P. Zamora, DFO, pers. comm.).

Finally, the American eel, a sister species of the European eel, is the 'host specimen of choice' (for comparison purposes), given that the bulk of literature on helminth communities in freshwater fishes is based on studies using the European eel. No comparable studies exist using the American eel. Furthermore, any information on the life cycles and population biology of metazoan parasites of American eel populations would be invaluble for the developing eel aquaculture industry.

2. METHODS

2.1 Study Site

Eels were collected from 8 sites throughout a 20 km long watershed in south western Nova Scotia (Figure 1). The entire catchment flows southward into Mahone Bay (44°40'N; 64°10'W) and is located in an area of poor drainage and shallow soil, underlain by granite and metamorphic rocks low in basic minerals; hence, the waters have a high acidity content (Watt and White, 1991). The watershed is somewhat unique: one-half (sites 2-7) received annual liming (by applying calcite limestone over the ice in winter) at the headwater lakes (sites 7,6 and 5) since 1986 as part of a DFO deacidification program, while the other half (site 8) was subject to natural conditions (Watt and White, 1991). Both drainage systems converge at site 1 (East River), located about 1 km from the ocean (Mahone Bay). The annual liming has raised the pH of sites 4 -7 from values below 5.2 (prior to 1986) to above 6.0 (Watt and White, 1991). Presently, the watershed has distinct pH and acidity gradients (Figure 2). The lowest pH was at site 8 (Connaught Lake) and its annual mean pH values were significantly less (ANOVA, $p < .001$) than those of all other sites. The highest pH was at site 6 (Timber Lake) and its annual mean ($\pm$ s.e.) pH (6.81 ± 0.05 in 1995; 6.73 ± 0.03 in 1996) was significantly higher (ANOVA, $p < 0.001$) than all other sites. There was a progressive decline in pH from site 6 down the catchment to site 1 (Figure 2). Despite slight monthly variation, there were no significant differences in mean pH between months. The mean pH per site in 1995 was significantly greater (t -test, $p < 0.05$) than that in 1996 (possibly a consequence of periodic flooding in 1996), but the same trends among sites were evident. Sites 2 - 8 were considered 'first-order' streams and

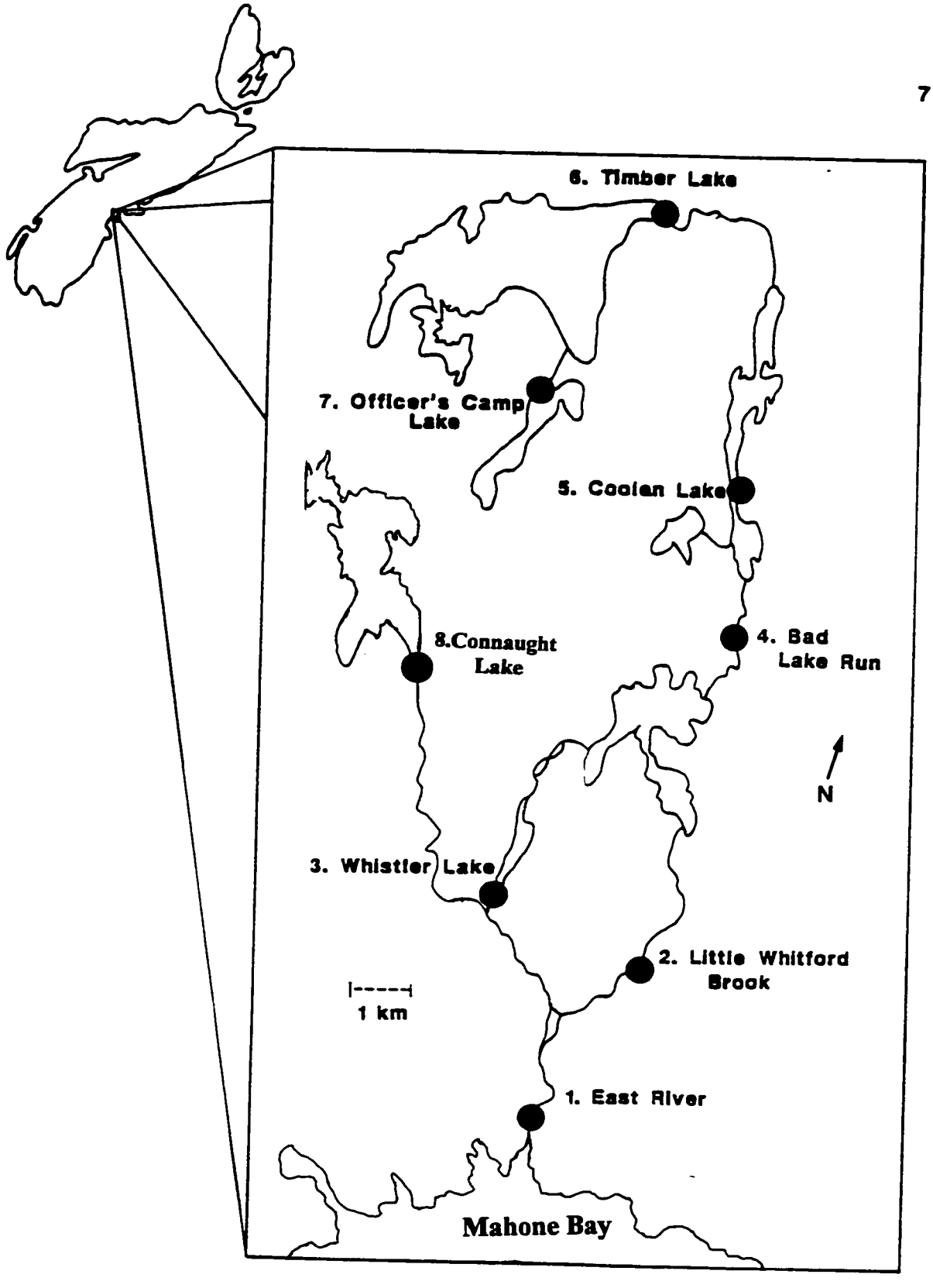


Figure 1. Map of the Timber Lake / Connaught Lake watershed, Nova Scotia, depicting 8 sites where eels were collected.

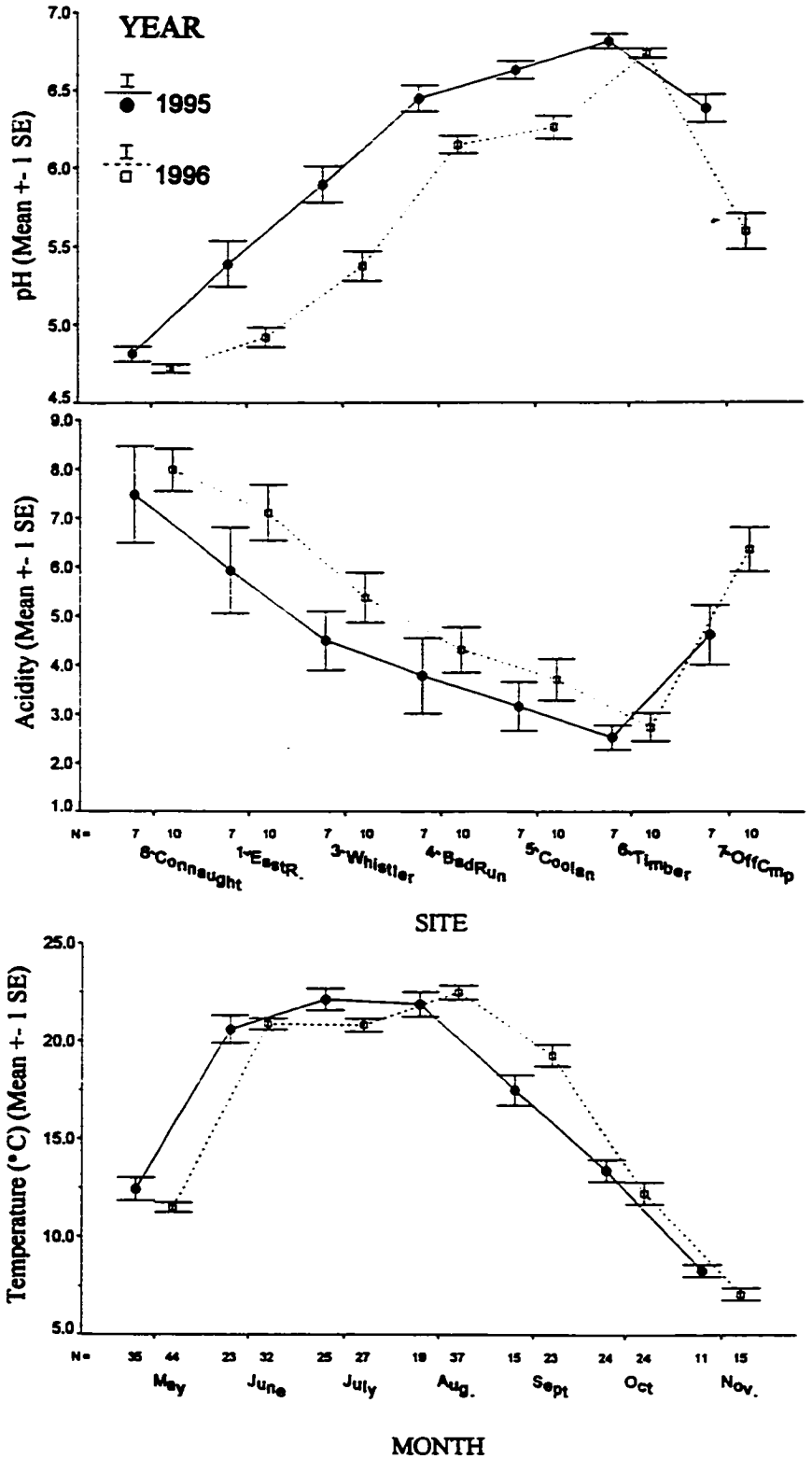


Figure 2. Annual mean (±s.e.) ph, acidity and water temperature for each sample site during 1995 and 1996. (Data provided by Mr. D. Ashfield, DFO,Halifax. No water chemistry analyses were performed at site 2 -Whitford Brook.)

site 1 was considered 'second order' (terminology follows Hynes, 1970).

There were no significant differences (ANOVA, $p > 0.10$) in mean water temperature among sites within each month, but mean monthly totals were significant (ANOVA, $p < 0.001$). The highest mean monthly water temperatures were in July and August ($21.44 \pm 0.33\,°C$ and $22.28 \pm 0.32\,°C$ respectively), while the lowest (during the sampling period) was in November ($7.61 \pm 0.25\,°C$; Figure 2).

All sites were bordered by alder, hardwood and softwood growth, but differed in flow rate, stream width, substrata and percent coverage by stream border vegetation (Table 1). Site 1 (East River) was the largest (10-21 m wide) and had the fastest flow rates (7.0 - 25.6 cm/s) over a predominantly boulder/cobble substrate. Such conditions often created sampling difficulties. Site 4 (Bad Lake Run) had similar flow rates compared to East River (moderate flow:5.0-22 cm/s) and similar substrate, but was much narrower and had a greater percent coverage by stream border vegetation (alder, softwood). Sites 2, 3 and 5 had similar flow rates (medium flow: 2.5-7.0 cm/s), similar substrata, but differed in size and percent coverage by vegetation (site 2 was the smallest of all sites and had the greatest percent coverage by stream border vegetation). Sites 6 and 7 had the lowest flow rates (0.2-3.0 cm/s), comprised mainly of pools, with similar substrata (pebble, gravel, sand), differing only in percent coverage by stream border vegetation and by the presence of a man-made dam at site 6. In times of flooding (spates), site 1 would rapidly increase in depth and flow rates, which converted already difficult sampling conditions into near impossible conditions. During the summer of 1996, Nova Scotia was subject to a series of 4 'tropical storms' / 'hurricanes' : (i) the first in July, exceeding mean rainfall by 96 mm; (ii)

Site	Stream Width (m)	Stream Type	Flow‡ (cm/s)	Area Fished (m^2)	% Cover by Vegetation	Substrate
1. East River	10.0 - 21.0	99% Riffle	7.0 - 25.6	819	0	boulder, cobble
2. Whitford Brook	1.0 - 3.0	25% Riffle 75% Pool	2.5 - 7.0	120	95	cobble, pebbles, gravel
3. Whistler Lake	3.0 - 15.0	40% Riffle 60% Pool	2.5 - 7.0	380	0	cobble, pebbles, gravel
4. Bad Lake Run	4.0 - 6.0	90%Riffle 10%Pool	5.0 - 22.3	480	75	boulder, cobble, pebbles
5. Coolan Lake	3.5 - 8.0	65% Riffle 35% Pool	2.5 - 7.0	253	10	cobble, pebbles, gravel
6. Timber Lake	2.5 - 3.5	20% Riffle 80% Pool	0.5 - 3.0	348	10	pebble, gravel, sand
7. Officer's Camp Lake	1.5 - 2.5	15% Riffle 80% Pool	0.2 - 2.5	230	15	pebble, gravel, sand
8. Connaught Lake	2.5 - 12	90% Riffle 10% Pool	5.5 - 17.6	350	0	boulder, cobble

Table 1. Physical characteristics of the sample sites within the Timber Lake watershed.

‡Flow Rate data for sites 1 and 6 provided by Mr. D. Ashfield, Halifax Regional Fisheries Lab. Flow rates for other sites were calibrated from surface current rate estimates using floating objects.

two in September, exceeding mean rainfall by 270 mm and (iii) the fourth in October, exceeding mean rainfall by 130 mm (Canadian Meterological Service, 1996). As a consequence, the annual mean water flow rate at site 1 was significantly higher ($p < 0.05$) in 1996 than that in 1995 (19.3 $\pm$ 1.2 cm/s and 10.2 $\pm$ 1.1 cm/s respectively; data from Mr. D. Ashfield, Halifax Regional Fisheries Laboratory). At the upper reaches of the watershed (site 6) there was no significant difference in mean annual flow rate, likely a consequence of the dam being able to regulate the spate level.

In addition to eels, a variety of other fishes were caught in the watershed: yellow perch (*Perca flavescens*; white sucker (*Catostomus commersoni*); common shiner (Luxilus (=*Notropis*) *cornutus*); killifish (*Fundulus diaphanus*); ninespine stickleback (*Pungitius pungitius*); brook charr (*Salvelinus fontinalis*) and Atlantic salmon (*Salmo salar*). The salmonids and white suckers were most common at sites of highest pH (sites 4 -7), while the perch were abundant in the unlimed portion of the watershed (site 8). The other species were present in similar numbers at sites 1-7. Adult white suckers were abundant in deeper water (> 1 m) except during spawning in early June, when they would often aggregate in pools and riffles less than 15 cm deep. Juvenile white suckers were abundant throughout the entire limed portion of the watershed.

2.2 Eel Collection

From May to November (1995 and 1996) eels were collected by electrofishing the lake mouths/stream segments and adjacent shoreline of sites 3, 5-8, and the riverine segments of sites 1, 2 and 4. (Site 8 was sampled only during 1996.) A defined area (Table 1) and common depth range (15 - 80 cm, mean = 40 cm) from each site would be fished

for a maximum of 2 hours, in an attempt to collect 30 eels for parasite analysis from each site per month. Within these 'defined areas', estimates of eel population density (number of eels/100 m^2) were calculated after each electrofishing session and monthly means per site were compared to test if there was any significant relationship between eel density and parasite prevalence. As an additional estimate of local eel population densities, a monthly catch per unit effort (**CPUE** = the number of eels caught/electrofishing time in hours) was calculated at each site. Supplemental data on eel population densities and relative abundance of other fishes (e.g. salmonids, catostomids and cyprinids) from sites 1-8 during 1995-1996 were provided by Mr. P. Zamora of the Halifax Regional Fisheries Lab.

The sample size of 30 eels was determined from a series of parasite species accumulation curves from data collected during preliminary sampling in October and November, 1994, at sites 3-8. These curves would peak and level after 10-15 eels were sampled from each site, indicating that most parasite species had been found. This sample size was doubled to 30 eels to further reduce the possibility of 'missing' a rare parasite. All eels were individually bagged and stored on ice until they could be frozen at the laboratory for subsequent necropsy.

During the sampling period of 1995 and 1996, the lacustrine habitats of sites 3 and 5 were sampled for eels using 'commercial-size' trap pots baited with white suckers (*C. commersoni*) and set (by boat) a minimum of 100 m from the electrofished zones in depths of 4 -7 m. After 24 hours, all pots (3 per site) were checked and often re-set, depending on numbers of eels caught. An attempt was made to collect a minimum of 10 eels from baited pots at each site per month. No sampling was done during winter months

(December-April) because of ice cover and difficulty of capturing eels as they submerge into the substrate and enter torpor.

2.3 Mark-Recapture Study

To assess site fidelity and degree of eel mobility within the watershed, 719 eels (375 in 1995; 294 in 1996) were individually tagged and released monthly (May to October) at each site. (Sites 2 and 8 were excluded from mark-recapture studies because of low eel abundances.) The same area used for eel collection would be electrofished for a maximum of 1 hour, and all eels collected would be tagged. Eels collected in baited pots from sites 3 and 5 in 1996 were also used in mark-recapture studies. Prior to tagging, each eel would be placed individually in a solution of anaesthetic (MS-222, 1:1000) and streamwater for 1 - 5 minutes (larger eels required more time). Small eels (< 15 cm) were given coded 'fingerling tags', which were sewn and tied through the dorsal skin, while larger eels (> 15 cm) were given coded 'anchor tags' (applied with a tagging gun) subcutaneously midway along the dorsal surface. In 1996, the total length (0.1cm) was recorded for each tagged eel. After tagging, each eel was placed in 'recovery' bucket of streamwater for 5 - 10 minutes, until they became active. These tagged eels were released from the shoreline, at a common reference point at each site, into the electrofishing area. During the first 2 weeks of each sampling month, eels would be collected for mark-recapture studies and during the latter 2 weeks, eels were collected for parasite analysis.

In August 1996, 31 tagged eels were transplanted along the watershed to assess homing behaviour. Using the same tagging procedures previously described, 11 eels

collected 2 km downstream of site 6 were transplanted upstream to site 6 and 20 eels collected 0.8 km downstream of site 7 were transplanted upstream to site 7. The 2 'new' sites (downstream of sites 6 and 7) were then included when electrofishing for tagged eels from August - November. In May and June, 1997, sites 3-7 were sampled 4 times by electrofishing (using the same procedures previously described) in an attempt to recapture tagged and transplanted eels.

2.4 Benthic Stream Macroinvertebrate Sampling

To determine if similar patterns existed for species richness and diversity between parasite component communities and free-living benthic macroinvertebrate assemblages, random samples of benthic stream macroinvertebrates were collected from the electrofished areas at each sample site. During August, 1996, 3 samples per site were randomly sampled for benthic macroinvertebrates using the 'kick up' method as described in Hynes (1970). A 1 m^2 sampling quadrant was used while one person would kick up the substrate and wipe rocks as a second person stood immediately downstream with a dipnet (0.6 mm mesh) and collected all suspended materials. This technique would continue until the entire substrate within the quadrant was suspended and all rocks wiped clean of animals; this procedure usually took 10 - 20 minutes. According to Hynes (1970), this technique is best for enumerating species (providing little information on microhabitat location) and produces consistent results. Each sample was individually stored in 10% formalin in plastic 1 litre bottles until later identification. Supplemental data on counts of macroinvertebrate orders from sites 4, 6 & 8 during 1988 -1995 were provided by Dr. N.

Watson of the Halifax Regional Fisheries Lab.

2.5 Sample Analysis

At necropsy, the following were recorded from each eel: total length (0.01cm), eviscerated weight (0.1g), liver (only in 1995) and stomach weights (0.1g). Lengths and weights were used in calculations of: (i) body condition factor = [(body weight / length^3) x 1000]; (ii) hepatosomatic index (HSI) = [(liver weight / body weight) x 100] and (iii) visceralsomatic index (VSI) = [(stomach + intestine weight / body weight) x 100] as outlined in Jessop (1987) to quantify growth and body condition. A sample of 218 eels were randomly selected and aged (years in freshwater) using sagittal otoliths cleared in 70% ethanol as per Vøllestad (1985). In addition, a second sample of 125 eels were randomly selected and aged (years in freshwater) using sagittal otoliths 'ground' and stained with toluidine blue as outlined in Richter and McDermott (1990). Eels were identified as being 'yellow' (sexually immature) or 'silver' (sexually mature) using criteria such as skin colour, eye diameter ratio (eye diameter in mm / total length in mm) and stage of gonadal development (examined microscopically) as per Tesch (1977) and Gray and Andrews (1970).

The gills, stomach, intestine, urinary bladder, swimbladder and visceral cavity were examined microscopically for metazoan parasites. All parasites from each eel were identified to species (where possible) and enumerated. Data on parasites from silver eels were analyzed separately from those in yellow eels collected at the same sample site. In addition, any prey items present in the stomach were identified to Order and enumerated

for subsequent dietary analysis using the modified graphical Costello (1990) analysis by Amundsen *et al.* (1996). In this method, prey abundance is modified to **prey specific abundance (%) = (Σ Si / Σ Sti) x 100**, where **Σ Si** is the sum of prey species "i" and **Σ Sti** is the total content (sum) of **only** those predators with prey species "i"; the Costello method uses **Σ St** (total content (sum) of **all** prey species) as the numerator. The **frequency of occurrence** = (number of stomachs where prey species "i" occurs / number of stomachs with any prey) remains unchanged. In the modified method, individual dietary specialization is more defined, as several prey taxa may have a prey specific abundance of 100%. However, with the Costello (1990) method, all values of prey abundance would add up to 100%. Plots of frequency of occurrence and prey specific abundance can be constructed to identify feeding strategy patterns (e.g. generalist or specialist) at both individual and population scales.

Stream macroinvertebrate samples were examined in a sieve tray (0.50 mm mesh), with the aid of a stereoscope, and organisms were classified to Order and Family using Pimentel (1967) and Lehmkuhl (1979), then enumerated for community analysis.

All statistical analyses were computed using SPSS™ for Windows™, while figures were prepared using SPSS™ for Windows™ and Harvard Graphics™. Mean values were compared using oneway ANOVA (with a multiple between-pair comparison using Tukey's least signficant difference) or the non-parametric Kruskal-Wallis test. Prevalences were compared using the G-test. Regression models were applied to eel length and age and length and weight data. At the infra-community (within one host) level, the following mean values were computed: (i) number of intestinal helminth species per eel; (ii) number

(infrapopulation) of intestinal helminths per eel; (iii) total number of metazoan parasite species per eel (including gill parasites) and (iv) total number (infrapopulation) of metazoan parasites (including gill parasites) per eel. In addition, tests of interspecific association and covariance (χ^2 and W-statistic, based on presence/absence and species abundance data respectively) were performed and three species association indices (Ochiai, Dice and Jaccard) were calculated using statistical software from Ludwig and Reynolds (1988).

At the helminth component community (within a host population) level, numbers of individual intestinal helminth species at each sample site (monthly) were used to compute: (i) Shannon index of diversity, $\mathbf{H'} = -\Sigma(pi\ lnpi)$; (ii) Simpson index of dominance, $\lambda = \Sigma pi^2$; (iii) Hill's number, $\mathbf{N2} = 1/\lambda$; and (iv) Pielou's index of Evenness $J' = H'/ \ln(S)$ using software from Ludwig and Reynolds (1988). To classify component communities based on helminth abundances, a cluster analyses (using relative Euclidean distances and the flexible method clustering strategy) were performed using Ludwig and Reynolds (1988). The flexible method of clustering is 'space-conserving': the clustering of additional sampling units at various distances introduces little distortion (e.g. dilation or contraction) when these distances are compared with the original data matrix distance (Ludwig and Reynolds, 1988). Furthermore, Ludwig and Reynolds (1988) recommend using $\beta = 0.25$ when using the flexible startegy as excessive negative or positive values could lead to dilation or contraction distortion respectively. To identify patterns among helminth component communities, using helminth abundances, correspondence analyses (indirect ordination) and multiple linear regression analyses (testing the influence of the

abiotic factors: pH, flow rate, and distance from sea on patterns of helminth community ordination) were performed using CANOCO™ software (Jongman *et al.*, 1996). The same formulae, classification and ordination procedures were applied to the stream macroinvertebrate assemblage data.

For this study, the term 'community' applies only to those helminths recorded from the stomach and intestine. This term does not imply any interaction, but is used because all species were collected from the same 'environment' within the host, and it is the term most widely used in the literature. If the metazoan parasites from the gills are included, the term 'parasite assemblage' will be used. The terms **prevalence** (percentage of hosts parasitized), **intensity** (number of parasites/number of infested hosts only) and **abundance** (number of parasites/ total number of hosts in a sample) are the same as those described in Margolis *et al.* (1982). The term **specialist** is applied to those parasites who attain sexual maturity only in eels, and **generalist** is applied to those parasites who may attain sexual maturity in a variety of fish species (Marcogliese and Cone, 1993).

3. RESULTS

3.1 Eel Biology - *Catch Statistics*

A total of 2070 eels (1051 eels in 1995, 1019 eels in 1996) were necropsied for parasite analysis (Table 2). Low water levels during late summer 1995 and periodic spates during late summer 1996 prevented the collection of 30 eels at each site per month. Estimates of eel population density and catch per unit effort (CPUE) varied slightly from month to month, with most density estimates in the range of 6-12 eels/100 m^2 (Figure 3a; b).

Monthly mean estimates of eel density were highest in June or July at all sites except site 8 (Figure 3a; b). High mean eel density estimates (~ 25-30 eels/100 m^2) and high CPUE values (~ 50 eels/hr) were recorded from site 6 (Timber) and site 2 (Whitford) during June and July as these sites had an abundance of small eels (8.0-15.0 cm). Additional increases in eel density and CPUE were recorded from site 1 (East River) and 3 (Whistler) during August and September and 'silver' eels were abundant in these samples.

From month to month, total mean eel density in July (6.89 ± 1.02 eels/$100m^2$) was significantly higher (ANOVA, $p < 0.001$) than that in May (3.79 ± 0.40 eels/$100m^2$) and October (3.14 ± 0.57 eels/$100m^2$). Site 1 (East River) had the lowest total mean eel density (2.45 ± 0.37 eels/$100m^2$), while the highest total mean eel densities were at site 2 (Whitford Brook; 10.38 ± 2.35 eels/$100m^2$), site 5 (Coolan Lake; 6.91 ± 0.55 eels/$100m^2$) and site 6 (Timber Lake; 7.73 ± 0.99 eels/$100m^2$). The high eel density at Whitford Brook was an ephemeral event which occurred in June of 1995 and 1996. Following a high eel density and CPUE in June, there was a rapid decline, such that it was impossible to obtain

Sample Site	MONTH May	June	July	Aug.	Sep.	Oct.	Totals
1. East River ('95)	30	30	28	17	9	0	114
('96)	30	30	16	0	18	0	94
2. Whitford Brook ('95)	23	30	14	12	0	0	79
('96)	21	29	11	0	0	0	61
3. Whistler Lake ('95)	30	30	30	30	29	29	178
('96)	30	30	30	30	22	23	165
4. Bad Lake Run ('95)	30	29	30	30	30	0	149
('96)	30	30	30	0	0	0	90
5. Coolan Lake ('95)	30	30	29	29	30	24	172
('96)	30	30	28	30	21	22	161
6. Timber Lake ('95)	30	28	30	30	30	30	178
('96)	30	30	30	30	30	30	180
7. Officer's Camp ('95)	29	30	21	17	0	0	97
Lake ('96)	26	30	29	17	0	0	102
8. Connaught ('96)	30	29	25	3	5	0	92
Potted eels ('95)	25	8	7	1	2	6	49
('96)	26	4	8	2	6	1	47
Silver eels ('95)	0	0	2	12	21	0	35
('96)	0	0	1	13	13	0	26
Totals ('95)	226	215	191	178	152	89	1051
('96)	236	243	235	121	108	76	1019

Table 2: Monthly sample sizes of eels collected for parasite analysis at each sample site during 1995 and 1996.

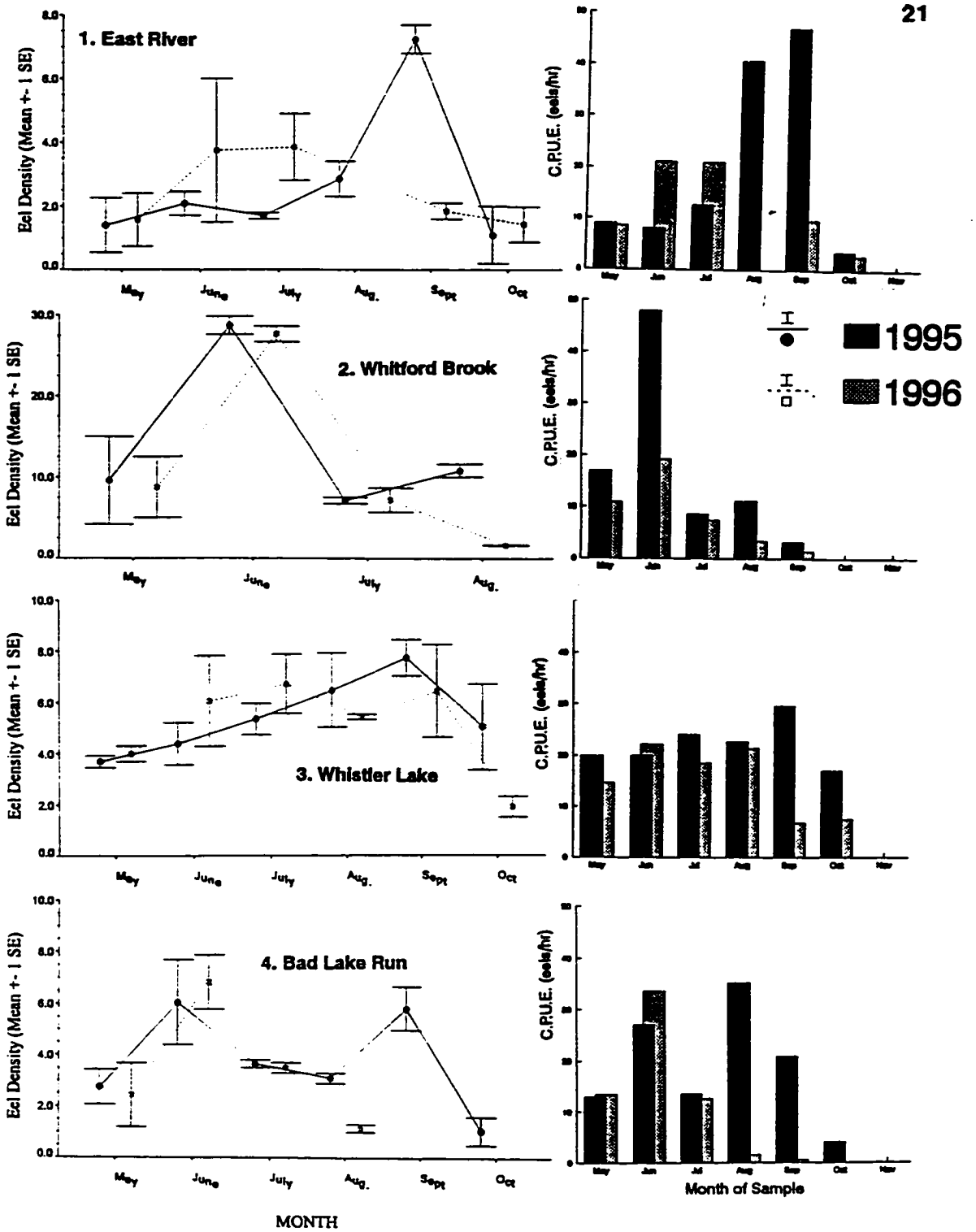


Figure 3a. Monthly mean (±s.e.) estimates of eel density (no. eels/100m²) and catch per unit effort (CPUE = no. eels/hr. electrofished) at sites 1-4 during 1995 and 1996.

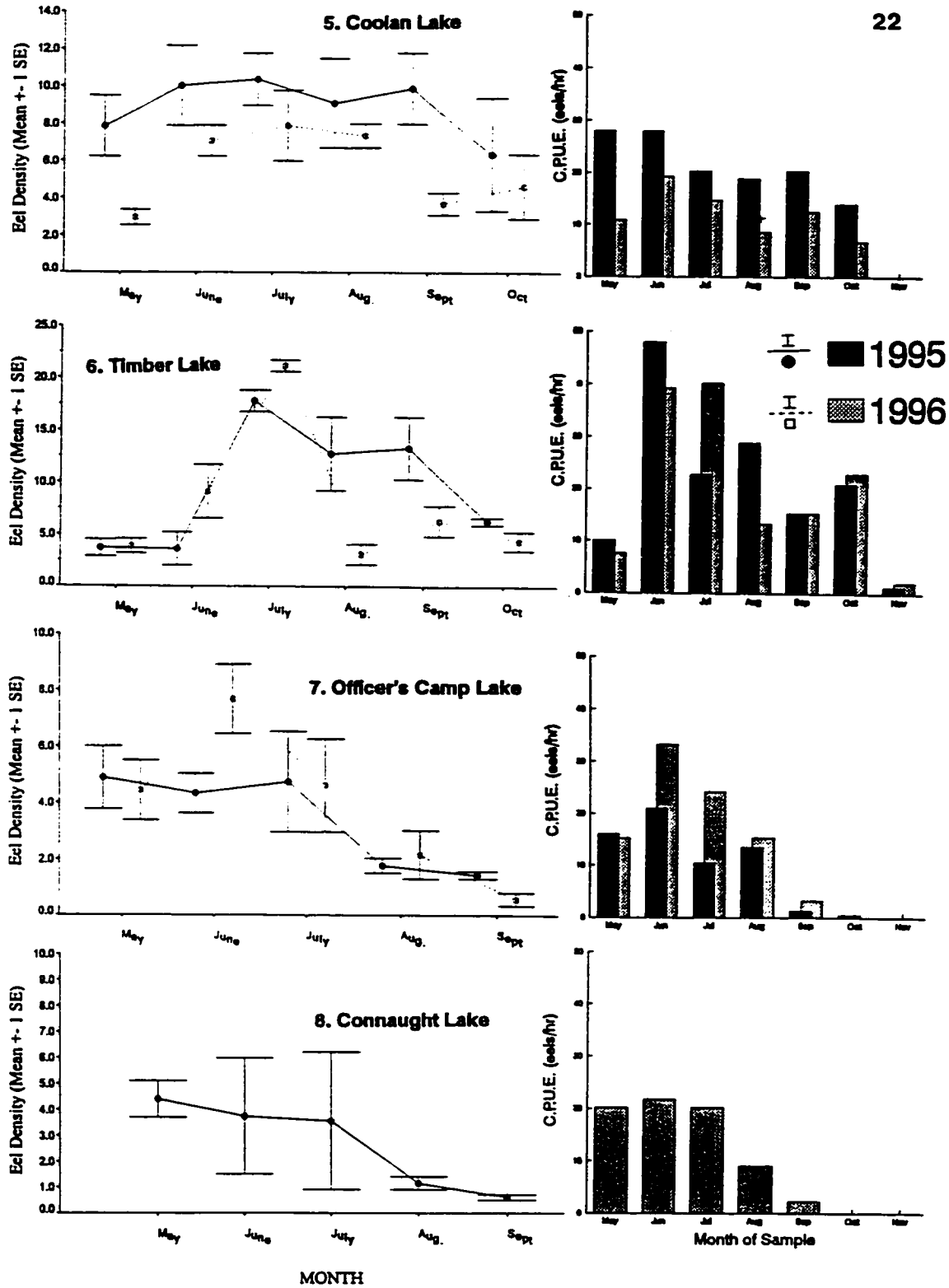


Figure 3b. Monthly mean (±s.e.) estimates of eel density (no. eels/100m²) and catch per unit effort (CPUE = no. eels/hr. electrofished) at sites 5-8 during 1995 and 1996.

30 eels from Whitford in any subsequent month (Table 2; Figure 3a). The results of eel density estimates and CPUE were very similar from year to year (Figure 3a; b) with 2 exceptions: sites 1 and 4 were subject to high spate levels and increased flow rates in 1996, making sampling near impossible, thus lowering CPUE. There was no significant relationship between distance from sea and eel population density estimates (Appendix A1).

Seaward migrating silver eels were collected during July, August and September (35 in 1995 and 27 in 1996) from sites 1-4 (Table 2). All but 6 (2 each from sites 2, 3 & 4) were collected at site 1 (East River). The sample of silver eels was dominated by males (85.7 % in 1995; 81.5% in 1996) whose mean length was 34.6 $\pm$ 0.2 cm, significantly less (t - test, $p < 0.05$) than that of silver females (47.9 $\pm$ 3.8 cm). In addition, the mean eye diameter to body length ratio was significantly larger (ANOVA; $p < 0.05$) in silver males (0.214 $\pm$ 0.006) than in silver females (0.146 $\pm$ 0.004) which was similar to yellow, sexually immature eels (0.147 $\pm$ 0.011).

Length Weight Relationship and Body Somatic Indices

Total length frequencies of eels collected per year were similar and there was no significant difference in the total mean length (23.44 $\pm$ 0.32 cm, 1995; 23.32 $\pm$ 0.33 cm, 1996; Figure 4). Most eels collected were 10-35 cm. The smallest eel collected was 6.0 cm in 1995 and the largest was 81 cm in 1996. The largest (ANOVA; $p < 0.001$) eels were those collected in baited pots (48.52 $\pm$ .93 cm, 1995; 46.92 $\pm$ 1.38 cm, 1996; Figure 5a), followed by sexually maturing silver eels (34.85 $\pm$ 0.52 cm, 1995; 37.81 $\pm$ 2.08 cm, 1996;

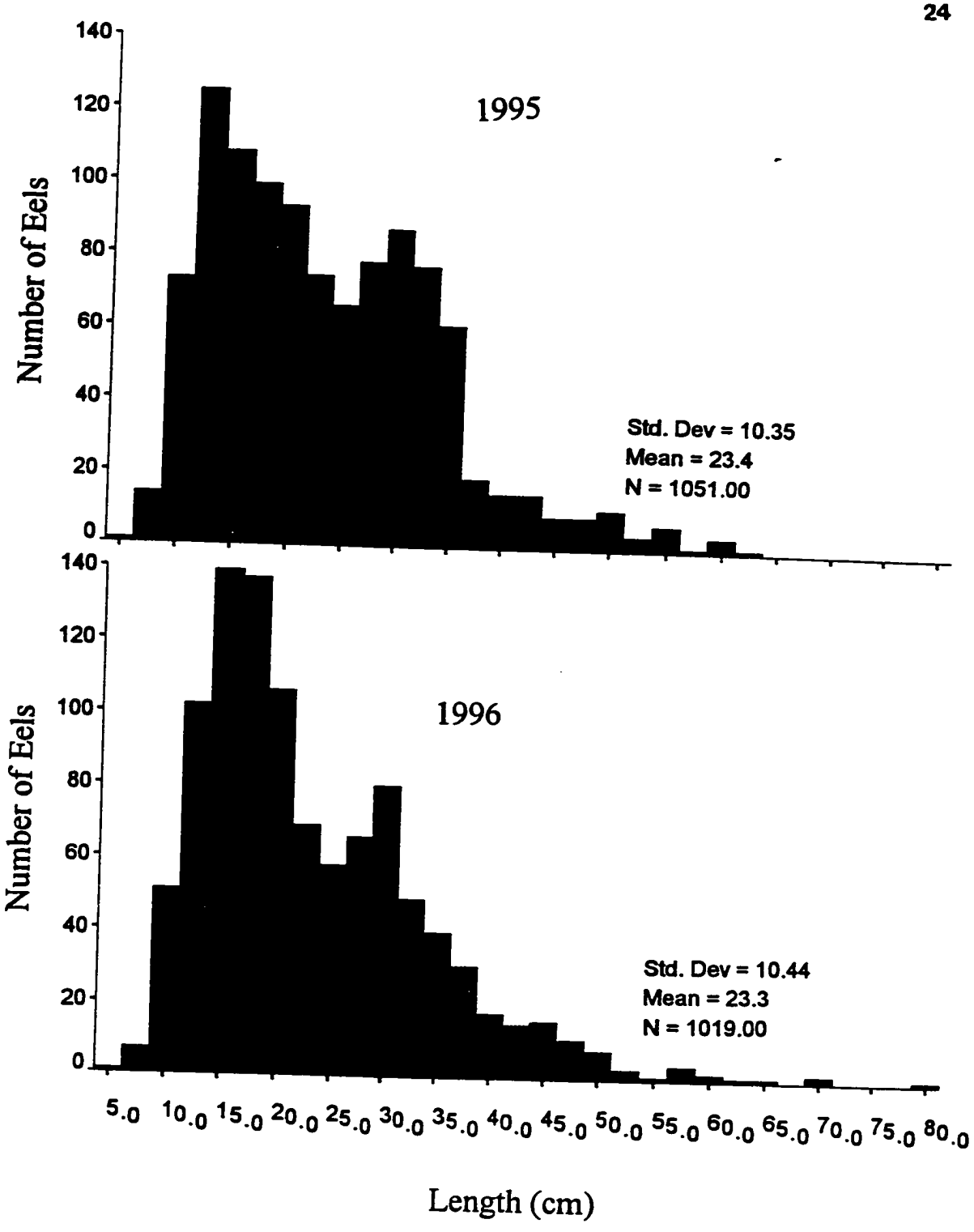


Figure 4. Length frequencies of all eels examined for parasite analysis during 1995 and 1996.

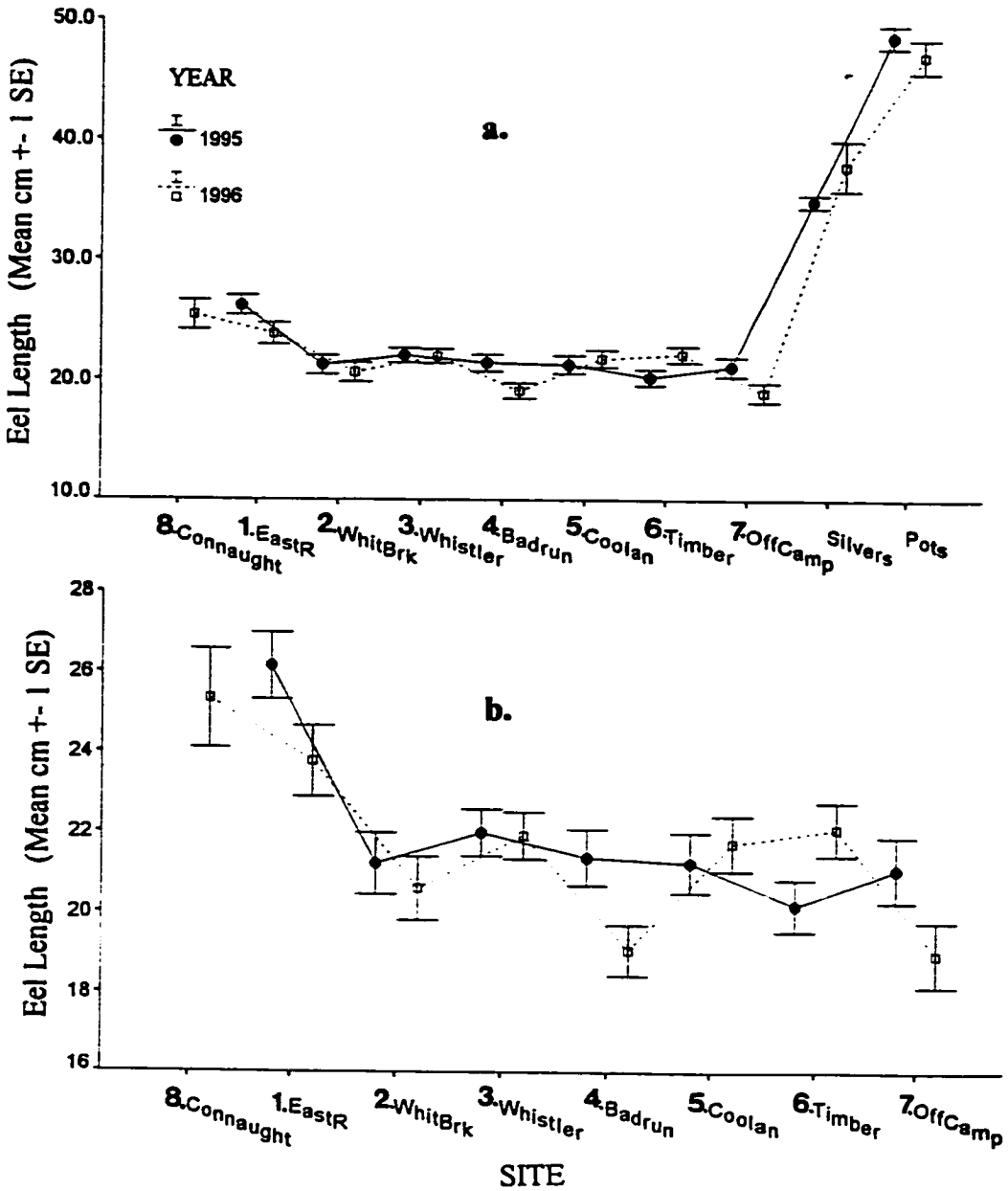


Figure 5. Total mean (±s.e.) lengths of : (a.) eels from each sample site, including silver and potted eels; (b.) electrofished eels only during 1995 and 1996.

Figure 5a). Among electrofished yellow eels, those from site 1 (East River) were significantly larger (ANOVA; $p < .05$) than those from sites 2-7 in 1995, and were significantly larger (ANOVA; $p < .05$) than those from sites 4 & 7 in 1996 (Figure 5b). Eels from site 8 (Connaught Lake) were significantly larger (ANOVA; $p < .05$) than those from sites 2,4,5 & 7 in 1996 (Figure 5b). There was no significant relationship between mean length of eels collected and time of sample (24hr or monthly) or distance from sea (Appendix A1). The total mean ($\pm$ s.e.) length of parasitized eels (26.13 $\pm$ 0.32 cm, n = 1183) was significantly greater (ANOVA; $p < 0.001$) than that of eels that were 'parasite free' (19.52 $\pm$ 0.26 cm, n = 887; Appendix A4-a).

Condition factor increased with eel length, such that from year to year, the annual mean condition factor of each eel length class was significantly larger (ANOVA; $p < 0.001$) than the previous class with 2 exceptions: (i) eels 35.1-40 cm and 40.1-45 cm were similar and (ii) eels 30.1-35 cm had the second highest condition factors (Appendix A2-a). The lowest annual mean ($\pm$ s.e.) condition factors were in eels < 10 cm (1.06 $\pm$ 0.02 in 1995; 1.05 $\pm$ 0.02 in 1996) and the highest in eels > 45 cm (1.74 $\pm$ 0.03 in 1995; 1.61 $\pm$ 0.05 in 1996). The total mean ($\pm$ s.e.) annual condition factor for potted (1.66 $\pm$ 0.03 in 1995; 1.56 $\pm$ 0.04 in 1996) and silver eels (1.61 $\pm$ 0.02 in 1995; 1.76 $\pm$ 0.03 in 1996) was significantly higher (ANOVA; $p < 0.001$) than that of eels from any sample site (Figure A2-b). Consequentially, these were also the largest eels sampled. Among electrofished eels only, the smallest annual mean ($\pm$ s.e.) condition factors were from site 6 (Timber; 1.14 $\pm$ 0.02 in 1995; 1.21 $\pm$ 0.02 in 1996) and 7 (Officer's Camp; 1.24 $\pm$ 0.02 in 1995; 1.21 $\pm$ 0.02 in 1996; Figure A1-c), and the majority (> 65%) of these eels were smaller than the

majority of eels from other sites. From month to month, there was a common trend among all sample sites whereby mean condition factors were lowest in May and increased over summer (Appendix A3). The mean (± s.e.) condition factor for parasitized eels (1.36 ± 0.01) was significantly greater (ANOVA; $p < 0.001$) than that for eels that were 'parasite-free' (1.21 ± 0.01; Appendix A4-b).

The visceralsomatic index was highest at both extremes of eel length classes (< 10 cm: 8.71 ± 0.33 in 1995; 10.46 ± 1.39 in 1996 and > 45 cm: 9.64 ± 1.80 in 1995; 7.74 ± 0.78 in 1996; Appendix A5-a). Other length classes had lower mean VSI values (~ 5.2-7.8), but were similar to each other (Appendix A5-a). The annual mean (± s.e.) VSI for silver eels (3.82 ± 0.24 in 1995; 2.97 ± 0.18 in 1996) was significantly lower (ANOVA; $p < 0.001$) than that of eels from any sample site; while the annual mean (± s.e.) VSI for potted eels (7.98 ± 0.66 in 1995; 10.20 ± 1.51 in 1996) was significantly higher (ANOVA; $p < 0.001$) than that of electrofished eels (Appendix A5-b). From month to month there was a common trend among all sample sites whereby mean VSI values were highest in May, and subsequentially decreased over summer (Appendix A5-c). There were no signfiicant differences in mean visceralsomatic indices between parasitized and 'parasite-free' eels.

The hepatosomatic index was highest (~ 2.2- 1.7) in eels less than 20 cm (ANOVA; $p < 0.05$), and was similar (~ 1.4-1.6) for eels larger than 20 cm (Appendix A6-a). The annual mean (± s.e.) HSI was significantly higher (ANOVA; $p < 0.05$) at site 2 (Whitford; 1.78 ± 0.06 in 1995) than at all other sites except site 1 (Appendix A6-b). From month to month, common trends were observed at each sample site, whereby mean

HSI values were highest in May, and decreased over summer (Appendix A6-c). The mean ($\pm$ s.e.) hepatosomatic index of parasitized eels (1.47 ± 0.02) was significantly lower (ANOVA; $p < 0.05$) than that of 'parasite-free' eels (1.55 ± 0.03; Appendix A4-c).

A simple linear model provided a weak fit ($r^2 = 0.684$) to an eel length weight relationship. A cubic model provided the best fit for any length weight relationship ($r^2 = 0.982$; Weight = 1.228(length) - 0.0646(length^2) + 0.0025(length^3) - 8.340; $p < 0.001$; Figure 6a). No differences were observed between male and female growth rates due to low sample sizes of sexually identifiable eels (silvers). Furthermore, a simple linear regression of log(length) and log(weight) produced a line of slope = 3.3; indicating that the formula for condition factor (weight/length^3) was applicable (Figure 6b).

Age Analysis

A simple linear model provided a good fit to both methods of age estimation : (i) Age = 0.2524(Length) - 0.3837, $r^2 = 0.9041$, $p < 0.001$ for alcohol cleared otoliths; (ii) Age = 0.4487(Length) - 1.752, $r^2 = 0.90649$, $p < 0.001$ for toluidine stained otoliths, (Figure 7). However, the linear model for age-length using alcohol cleared otoliths predicts lower ages for eels above 20 cm than does the model using toluidine stained otoliths. From the model based upon alcohol cleared otoliths, the oldest eel (81 cm) collected had resided in freshwater for 20 years, while the youngest (6 cm) was in its first year of freshwater residence. The model using toluidine stained otoliths predicts 34.5 years and in its first year of freshwater residence for these same respective lengths. The first model predicts that the majority of eels collected (10-35 cm) were freshwater

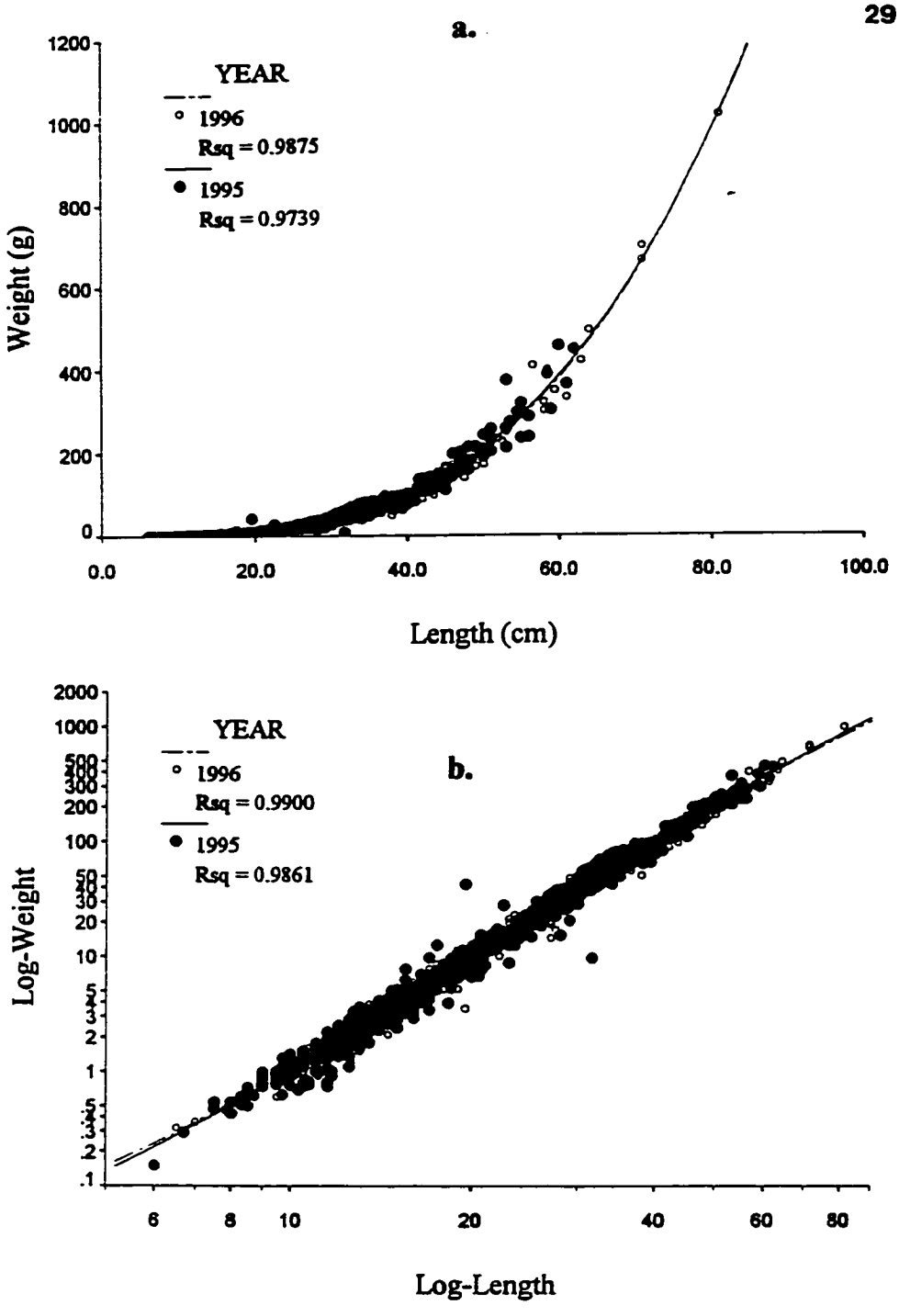


Figure 6.. Eel length weight relationship using : (a.) cubic model; (b.) logistic model.

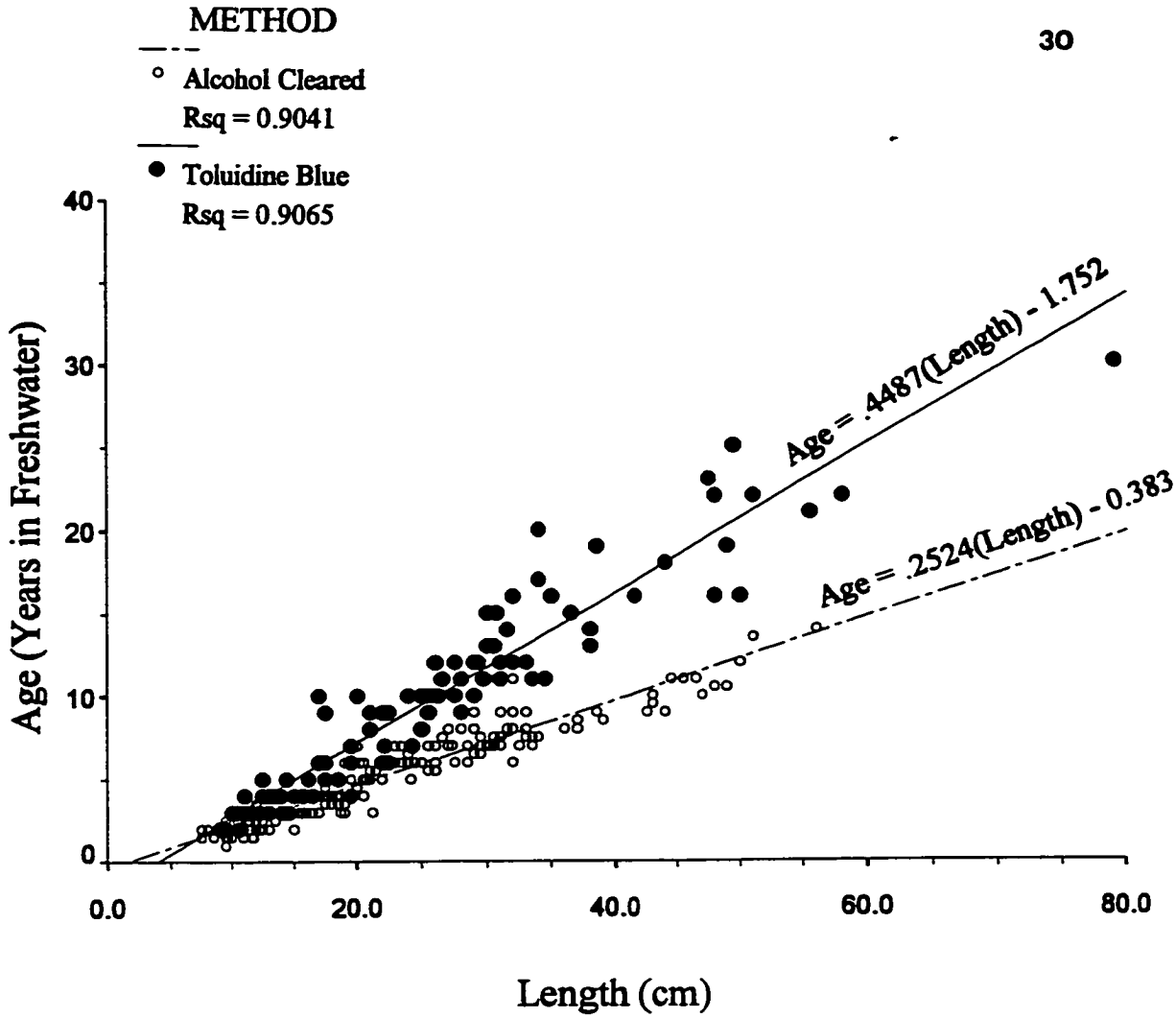


Figure 7. **Simple linear regression models of eel length (cm) and age (years in freshwater) using (○) alcohol cleared otoliths and (●) toluidine-blue stained otoliths.**

residents for 2 to 8 years, while the second model predicts that these eels were residents from 2 to 14 years.

Validation of these models, based on changes in length of recaptured tagged eels, suggest that both models predict larger lengths than was observed. However, the toluidine blue method predicts lengths that are 1.61 ± 0.14 cm larger than actual and the alcohol clearing method predicts lengths that are 3.21 ± 0.17 cm larger than actual. Recaptured tagged eels, previously measured, had an annual difference in length ranging from 0.0 to 5.5 cm.

Eel Diet

A total of 919 eels (44.3 %), ranging in length from 6.7 cm to 52.3 cm, had prey of various stages of digestion in their stomach. Eels collected in commercial pots were excluded from analyses because most stomachs contained bait. A total of 13 prey types were identified : (a) Annelida - Hirudinea (leeches); (b) Mollusca - Bivalvia (clams) and Gastropoda (snails); (c) Arthropoda - Crustacea (Amphipoda); (d) Arthropoda, Insecta - Odonata (dragonfly and damselfly naiads), Ephemeroptera (mayfly naiads), Plecoptera (stonefly naids), Hemiptera (adult bugs), Trichoptera (caddisfly larvae), Coleoptera (adult & larval beetles), Diptera (fly and mosquito larvae); (e) Osteichthyes - Cypriniformes (suckers and shiners), Anguilliformes (elvers). During 1995 and 1996, the most common prey items were Ephemeroptera (31%), Trichoptera (21 %), Odonata (20%), Diptera (18%) and Amphipoda (14%; Table 3). Hemiptera, Coleoptera and Gastropoda were the rarest prey (< 2.0%; Table 3). Arachnids (spiders) and Lepidoptera larvae (caterpillars)

Prey Taxon	1995 (%)	1996 (%)
Annelida		
Hirudinea	1.5	2.1
Mollusca		
Bivalvia	1.4	2.0
Gastropoda	0.2	0.3
Arthropoda		
Amphipoda	15.3	13.2
Odonata	19.4	21.9
Ephemeroptera	28.1	36.3
Plecoptera	7.5	13.8
Hemiptera	1.4	0.9
Trichoptera	18.7	25.9
Coleoptera	1.3	0.6
Diptera	21.6	15.5
Osteichthyes		
Cypriniformes	4.8	5.5
Anguilliformes	3.9	4.3

Table 3. Overall frequency of occurrence (%) of prey taxa recorded from the stomach of eels collected during 1995 and 1996.

were found in 4 eels but were excluded from analyses as these were terrestrial animals that had fallen into the water.

There were differences in the frequency of occurrence of prey items and mean number consumed by eels among the various sites. The molluscs (Bivalvia and Gastropoda) were present only at the sites of greatest pH (sites 3-7). Amphipods were absent from eels collected at the most acidic sites (1 & 8). The annual frequency of occurrence and mean number of amphipods consumed was significantly higher (ANOVA; $p < 0.001$) at site 3 (Whistler; Figure 8). Stonefly naiads (Plecoptera) were common in the diet of eels from sites with high flow rates (sites 1 & 4) and the mean number consumed was significantly higher (ANOVA; $p < 0.001$) than that at any other site (Figure 8). Diptera larvae were consumed most often and in the highest amounts (ANOVA; $p < 0.001$) at site 6 (Timber Brook; Figure 8). Eels at the most acidic site (Connaught) had a significantly higher (ANOVA; $p < 0.001$) mean amount of larval Trichoptera in their stomachs than eels at the other sites (Figure 8). Ephemeroptera naiads were most common in the diets of eels collected from the most acidic sites (Figure 8).

Trichoptera, Odonata and fish were most commonly consumed by larger eels (> 30 cm), while Amphipoda and Diptera dominated the diet of smaller eels (< 15 cm; Figure 9a). On a monthly comparison, Ephemeroptera dominated the diets of eels from all sites in May, while Diptera, Odonata and Amphipoda were most common in late summer-early fall (Figure 9b).

Variations in prey consumed among individuals was evident when the entire prey assemblage consumed by a population of eels at one site was analyzed using ecological

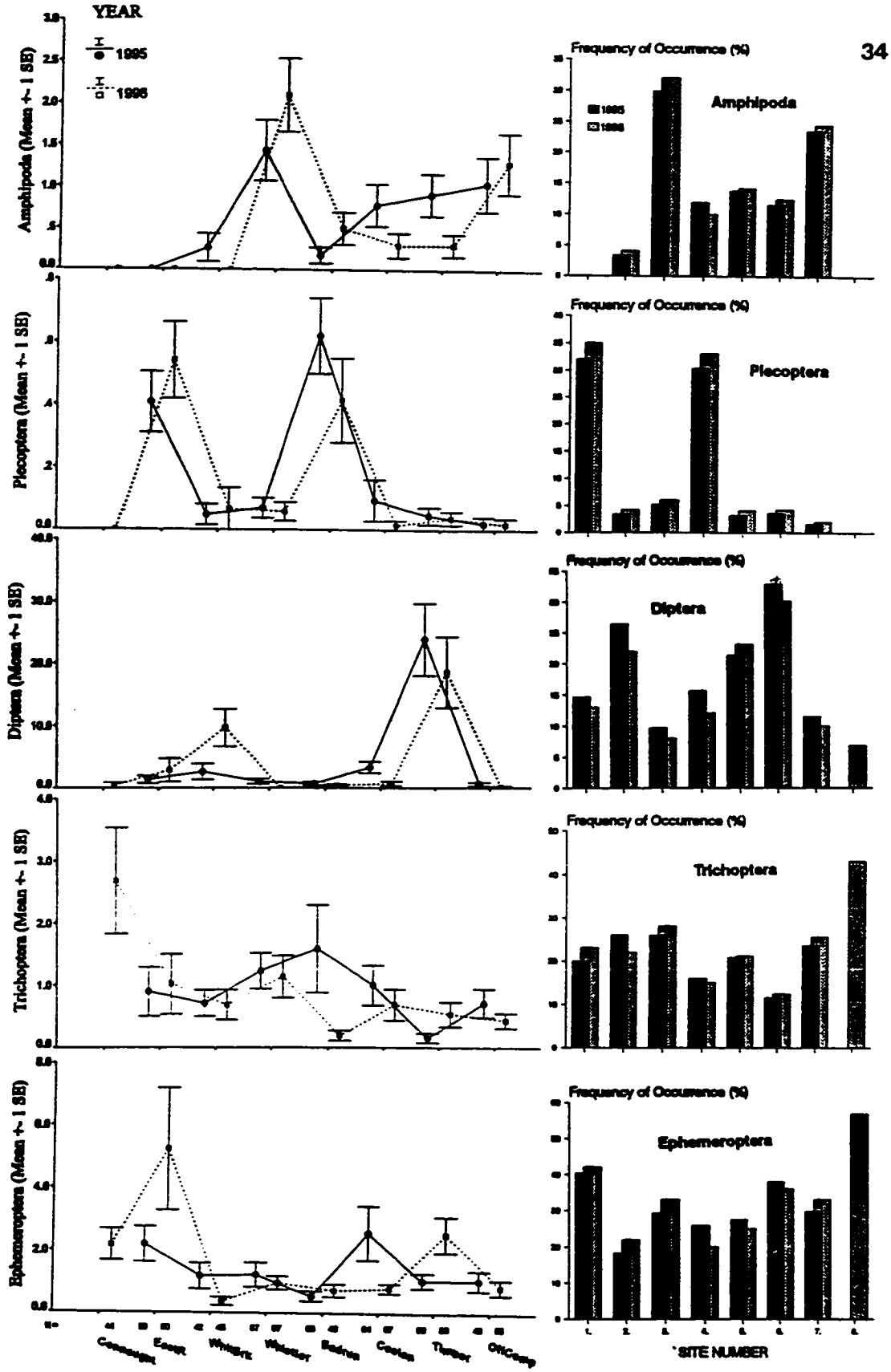


Figure 8. Annual mean (± s.e.) number of prey consumed and frequency of occurrence (%) at each sample site during 1995 and 1996.

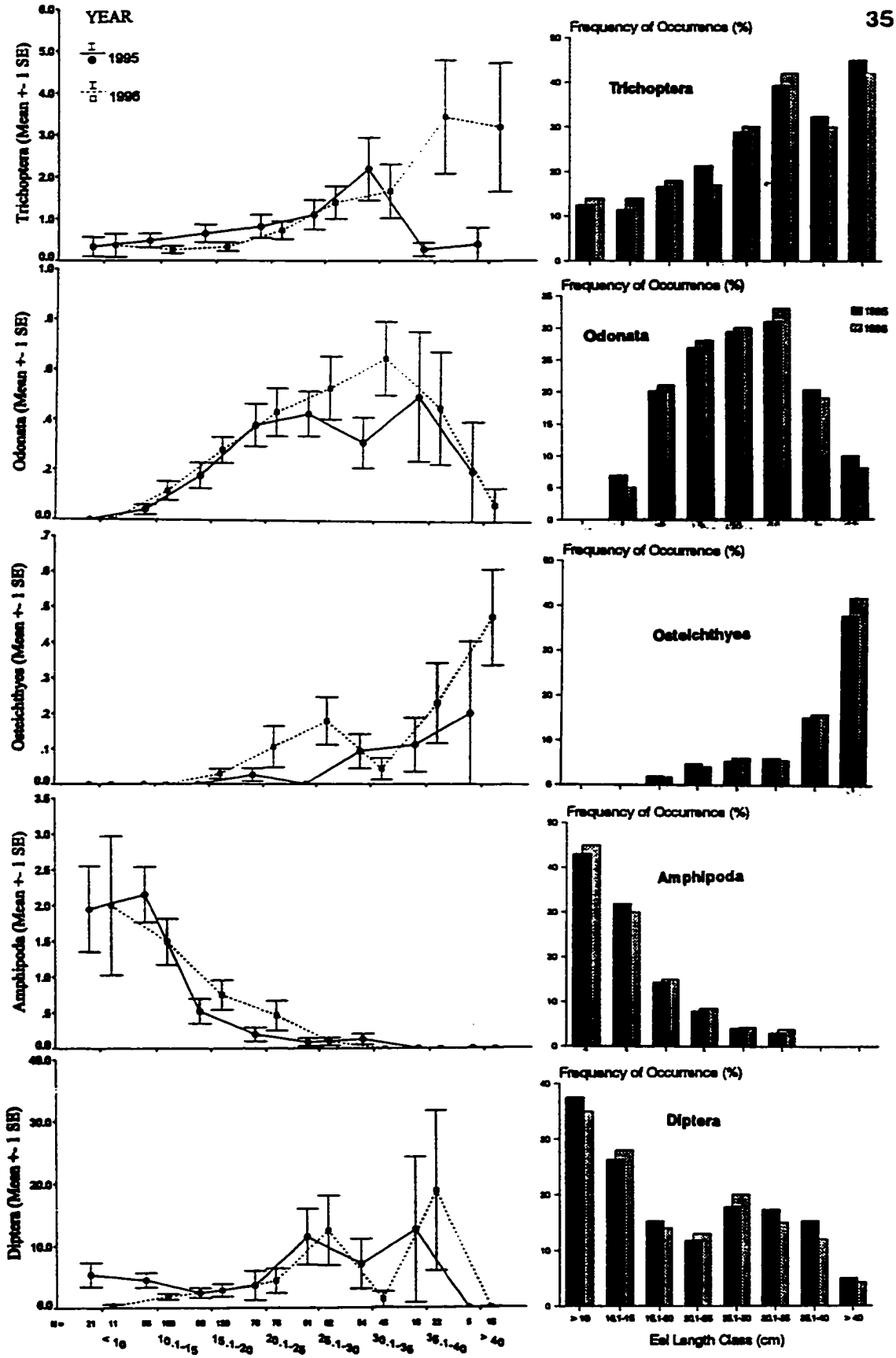


Figure 9a. Annual mean (± s.e.) number of prey consumed and frequency of occurrence (%) for each eel length class during 1995 and 1996.

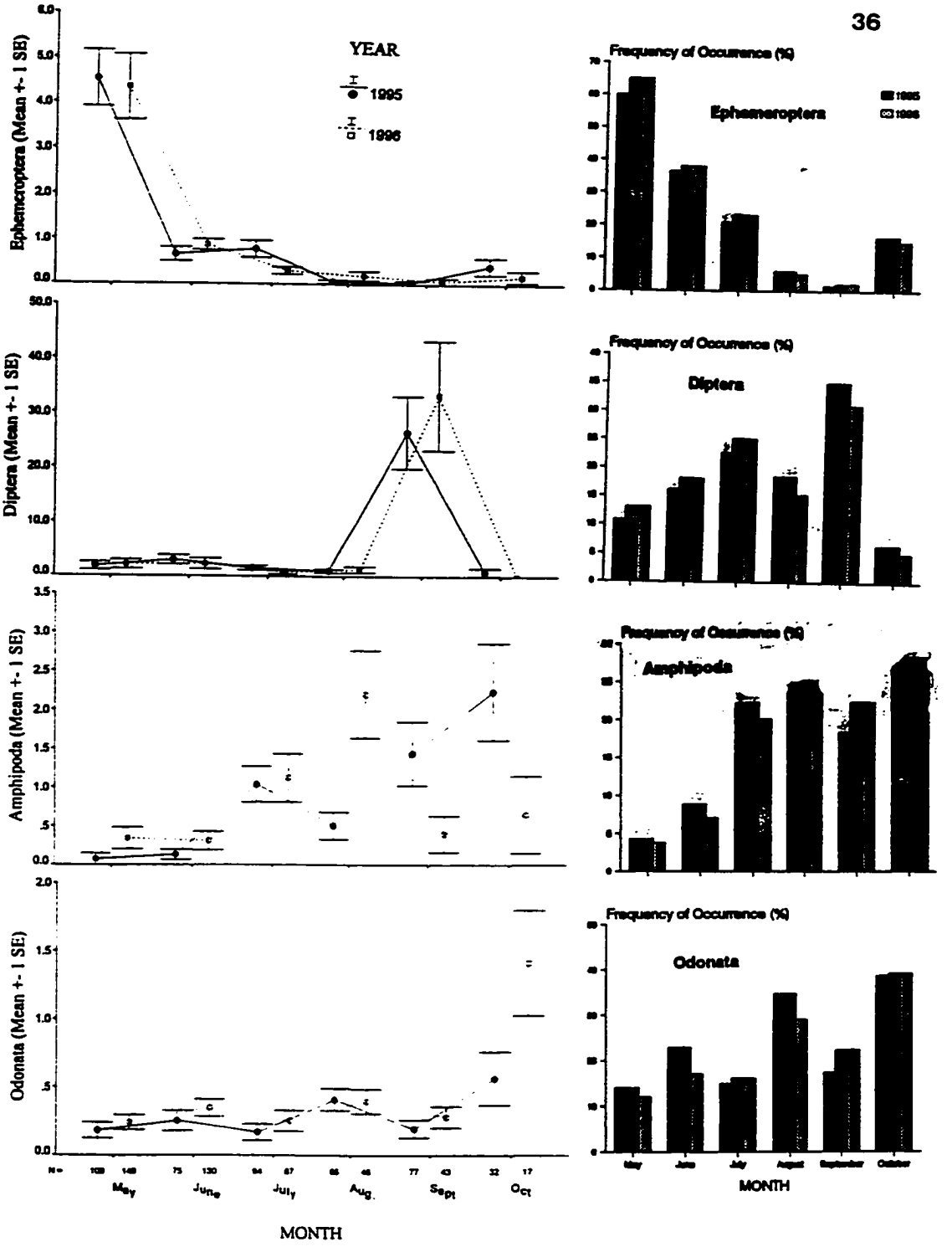


Figure 9b. Monthly mean (± s.e.) number of prey consumed and frequency of occurrence (%) during 1995 and 1996.

indices. Eels at the lowest pH sites (East & Connaught) had diets characterized by low diversity (Shannon Index, Hill's N2), low evenness and high dominance (Simpson Index; Figure 10). Overall, diet of small eels (<10 cm) and large eels (>35 cm) had lower mean prey richness and diversity indices, coupled with high mean dominance indices (Figure 11a). Small eels usually consumed either amphipods or Diptera larvae while the larger eels tended toward piscivory. On a monthly scale, the prey assemblage diversity was greatest in mid-summer (July, August) and lowest in May, September and November (Figure 11b).

Results of the modified Costello (1990) analysis indicate high values of prey specific abundance and low values of frequency of occurrence for each prey item and for each sample site (Figure 12a; b). This pattern is characterized by a clumping of points in the upper left corner of both plots.

Each eel stomach with prey usually contained only one prey item (83% in 1995; 69% in 1996; Appendix A7-a) and if several prey were present, one type often dominated. Rarely would the prey of one individual be found in equal numbers. Variation in the mean number of different prey species among the different eel length classes (Appendix A7-b) and among each sample site (Appendix A7-c) was low.

Mark-Recapture Study

In 1995, 45 (12%) tagged eels were recaptured, while in 1996, 33 (11.2%) tagged eels were recaptured. No tagged eel was recaptured at a different site from where it was initially caught, tagged and released. The total percentage of recaptured eels at all sites was very similar (~ 8-15%) during 1995 and 1996 (Figure 13a). Tagged eels

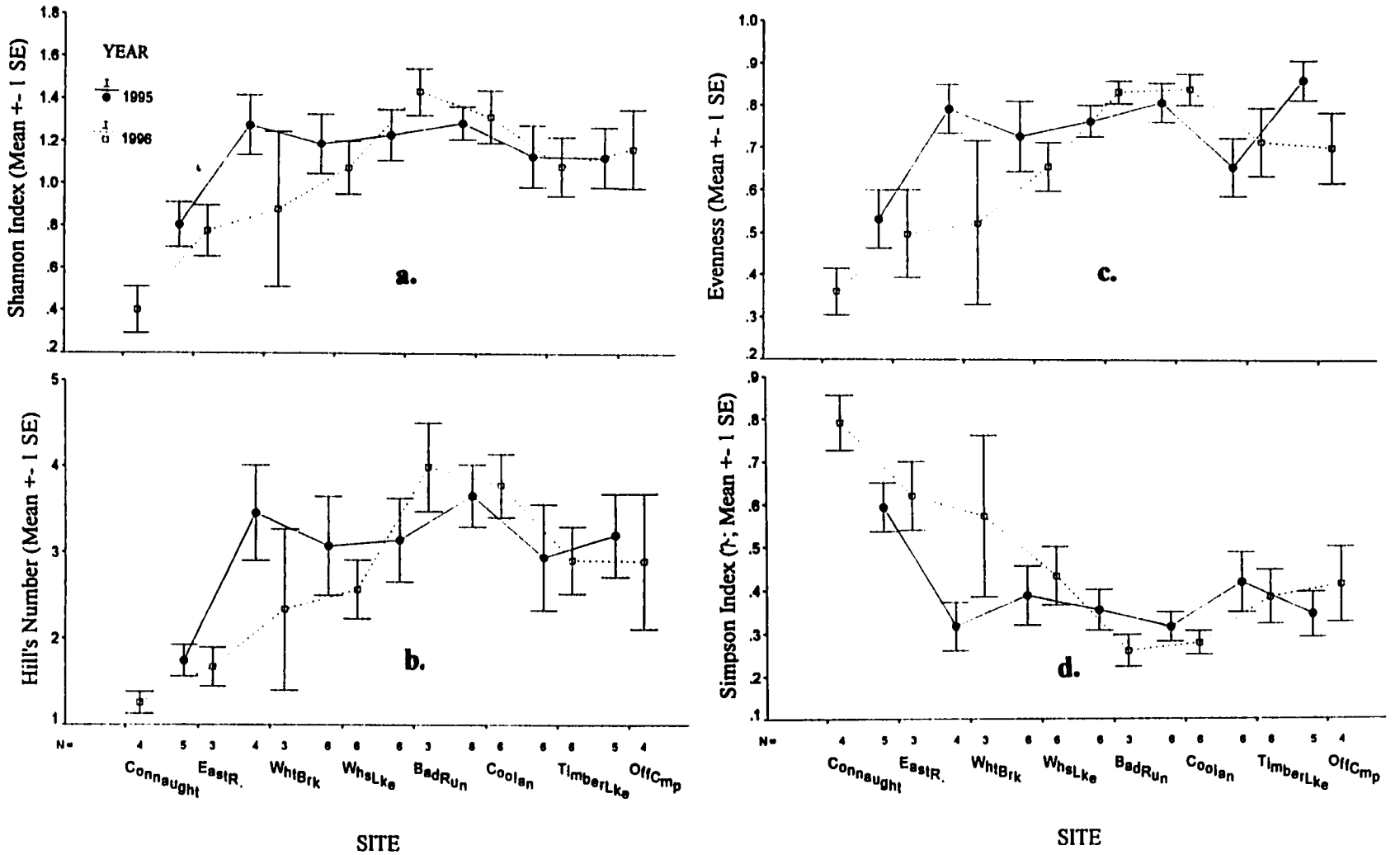


Figure 10. Annual mean (± s.e.) ecological indices : (a.) Shannon Index (H'); (b.) Hill's Number (N2); (c.) Pielou's Index of Evenness; (d.) Simpson Index (λ) for prey assemblages consumed at each sample site during 1995 and 1996.

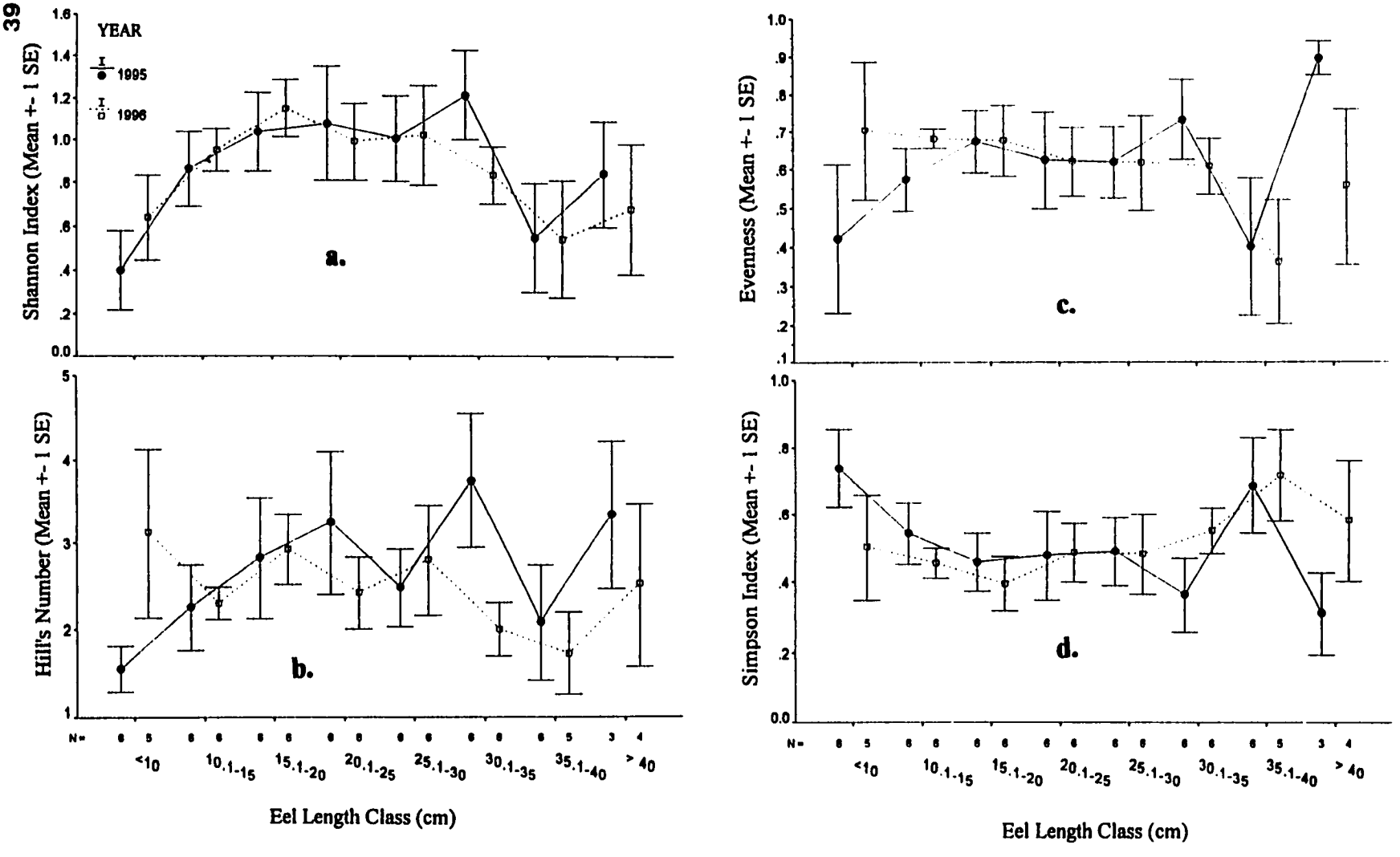


Figure 11a. Annual mean (± s.e.) ecological indices : (a.) Shannon Index (H'); (b.) Hill's Number (N2); (c.) Pielou's Index of Evenness; (d.) Simpson Index (λ) for prey assemblages consumed by each eel length class during 1995 and 1996.

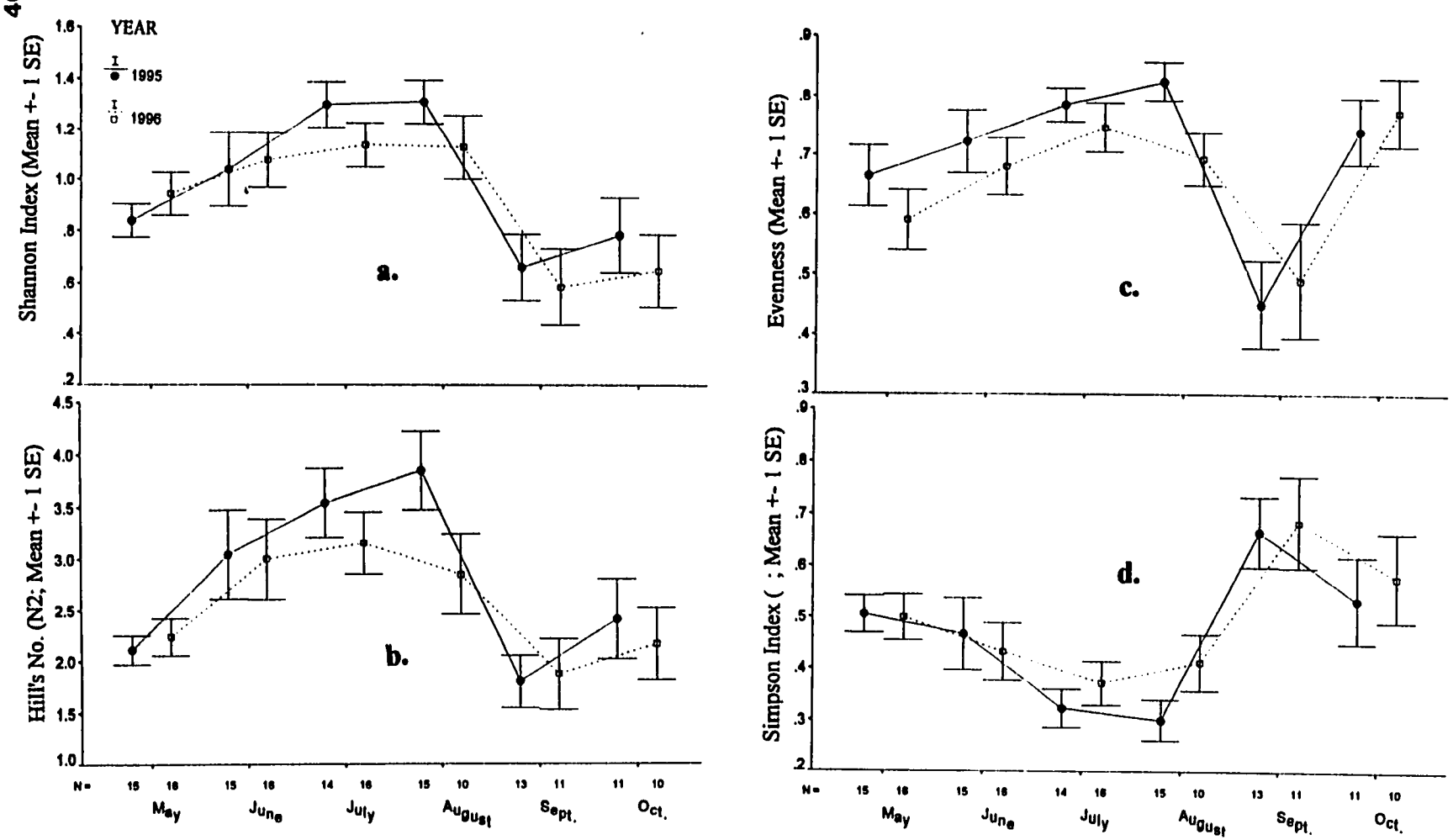


Figure 11b. Monthly mean (± s.e.) ecological indices : (a.) Shannon Index (H'); (b.) Hill's Number (N2); (c.) Pielou's Index of Evenness; (d.) Simpson Index (λ) for prey assemblages consumed during 1995 and 1996.

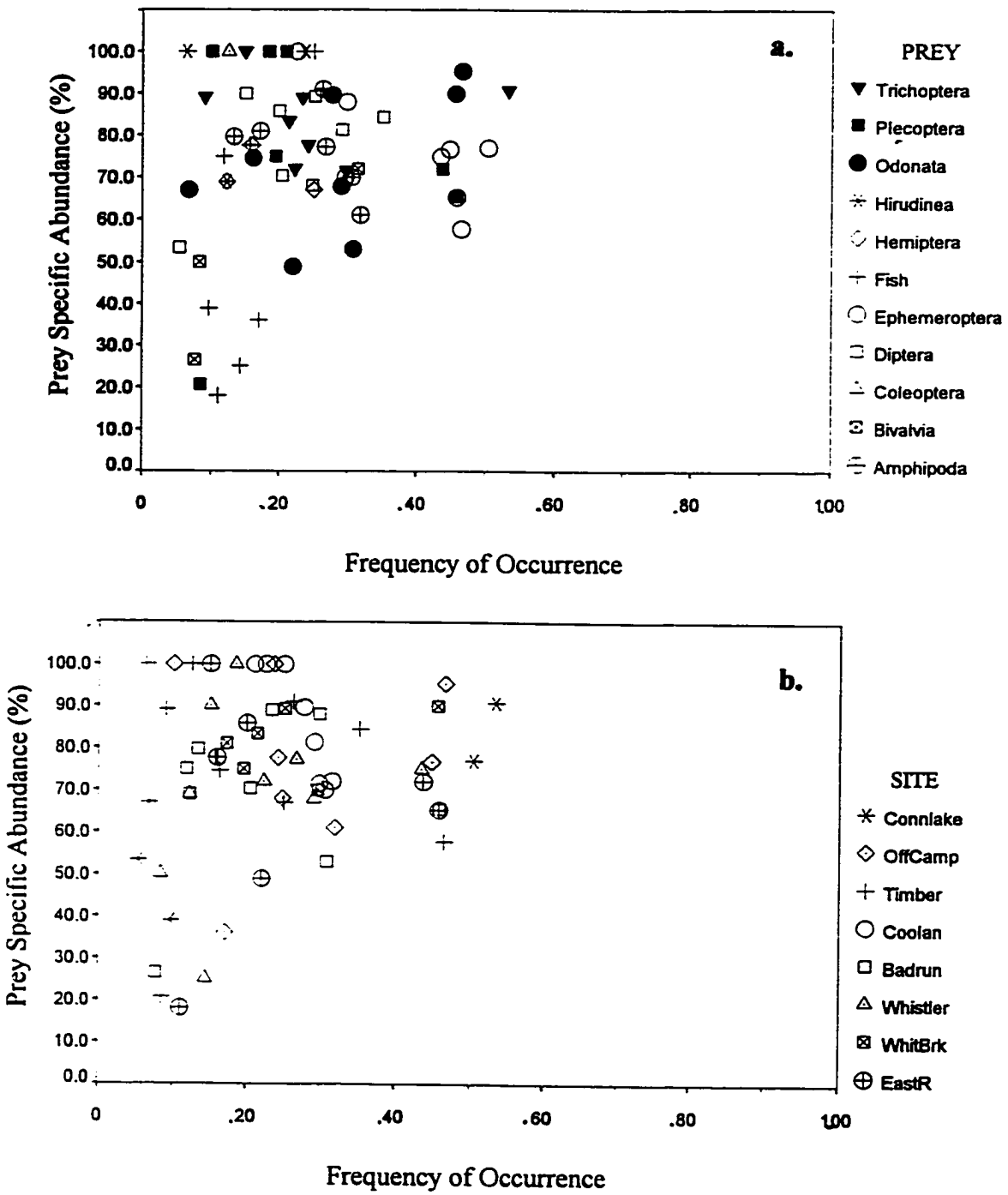


Figure 12. Prey specific abundance (%) and frequency of occurrence plots for : (a.) means of each prey type consumed and (b.) means of total prey consumed each sample site. (Data from 1995 and 1996 pooled.)

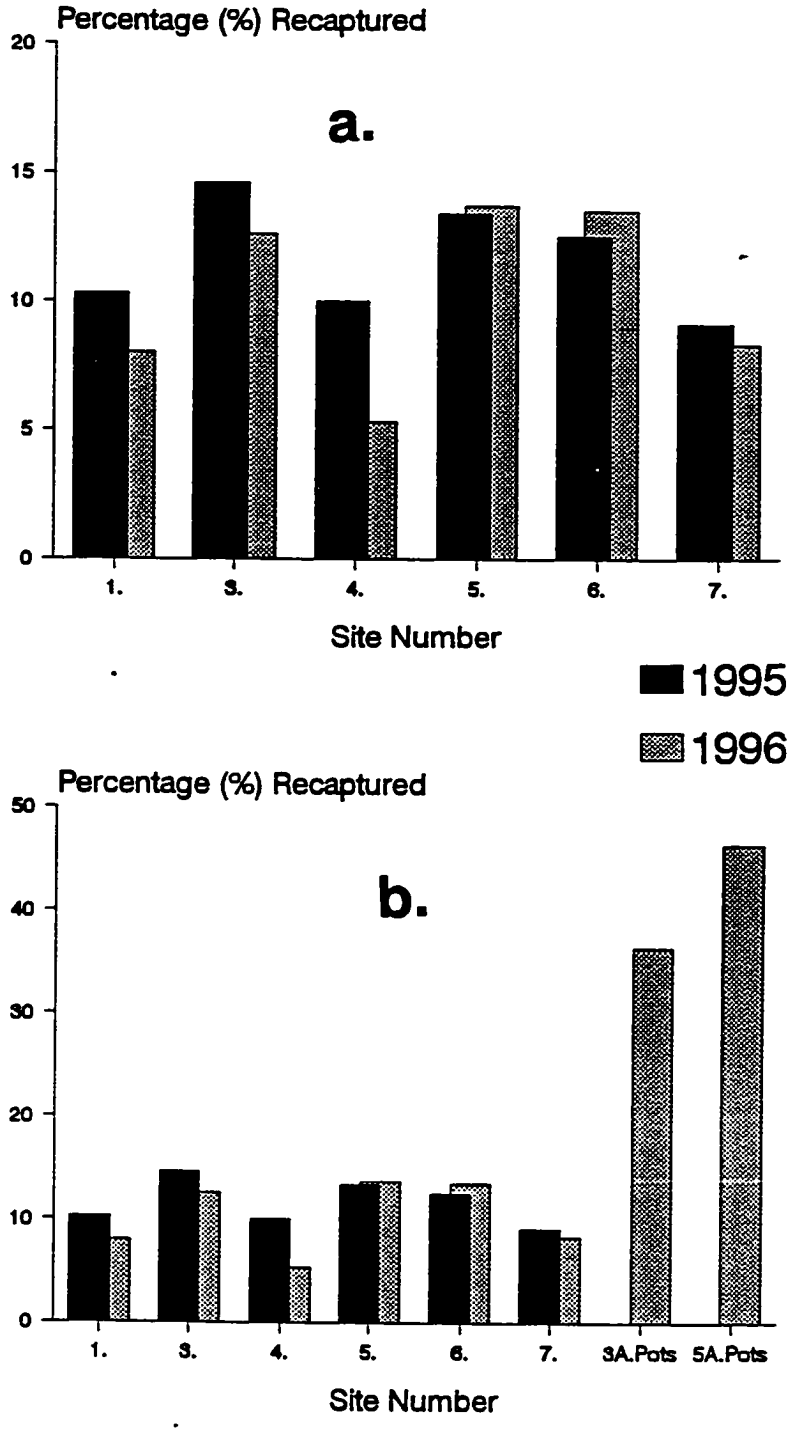
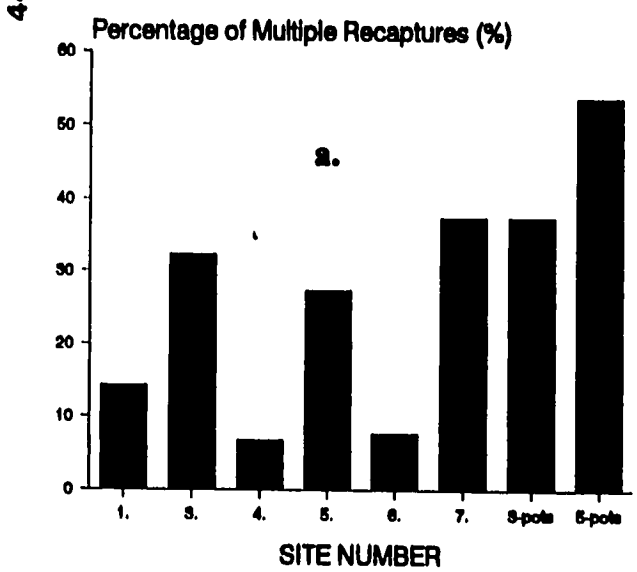


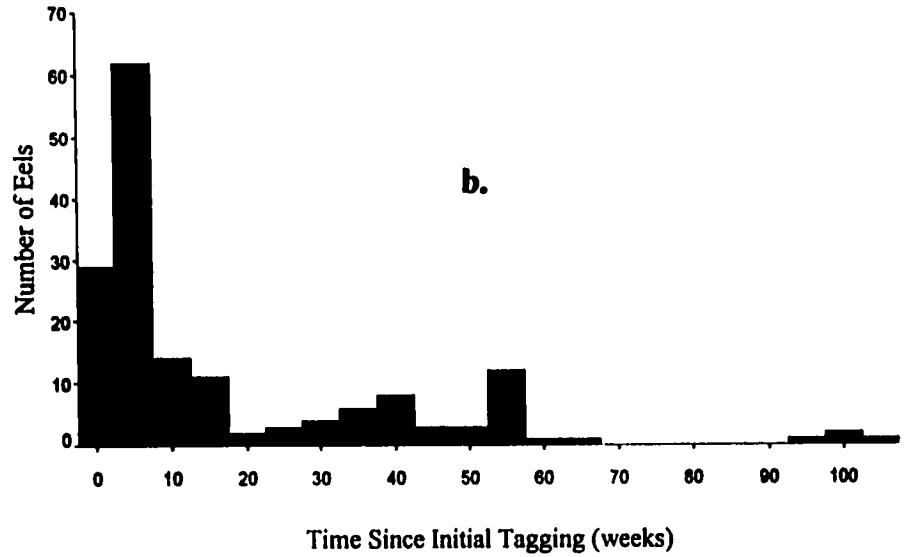
Figure 13. Total percentage (%) of recaptured eels at : (a.) electrofished sites only and (b.) electrofished and potted sites during 1995 and 1996.

collected in pots had the highest percentage of recaptures (36.4% at Whistler and 46.4% at Coolan; Figure 13b).

Eels were released and recaptured at all sites. However, site 3 (32.3%), site 5 (27.3%) and site 7 (37.5%) had the highest percentages of repeat recaptures (Figure 14a). Site 3 had one eel recaptured 4 times and 3 eels recaptured 3 times (at the same site) over the two years of the study. One eel each at sites 4 and 5 was recaptured 3 times from the same site. The remaining eels were recaptured twice over the sampling period. Potted eels had slightly higher percentages of multiple recaptured eels (37 % at site 3; 53.8% at site 5). One potted eel from site 5 was recaptured 6 times from the same location during the summer of 1996, then was taken for parasite analysis in September 1996. Most of the other multiple recaptured potted eels were caught 3 or 4 times at the same location. Interestingly, of those eels collected in pots and tagged, none were recaptured at the same site by electrofishing; however, 3 eels (2 from site 5; 1 from site 3; all > 40 cm) that were initially caught by electrofishing and tagged, were later caught in pots at these same sites.

Most tagged eels were recaptured 5-8 weeks after initial tagging (Figure 14b). The longest time between initial tagging and recapture was 739 days: a 31.5 cm long eel from site 4, initially tagged in June, 1995 and recaptured in June, 1997. Four other eels (2 from site 3, 1 each from sites 4 and 5) had comparable times (660- 690 days) between initial tagging and recapture. The shortest time to recapture was 5 days: a 49 cm long eel from site 3 was tagged June 12, 1996 and recaptured (in a pot) on June 17, 1996. Among electrofished eels, site 4 had the longest mean ($\pm$ s.e.) recapture time (36.45 $\pm$ 3.29 weeks; Figure 14c). Site 1 (East River) had the lowest mean ($\pm$ s.e.) recapture time (5.76





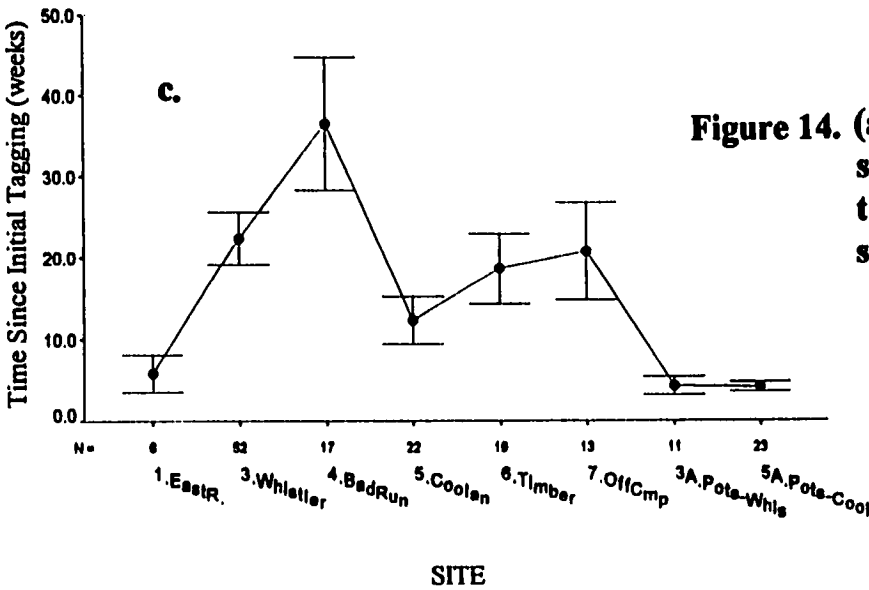


Figure 14. (a.) Percentage of tagged eels recaptured more than once at each sample site; (b.) frequency distribution of tagged eel recapture times and (c.) mean (± s.e.) recapture time of tagged eels at each sample site.

± 2.27 weeks, over 2 years) which was similar to that of tagged eels collected in pots (~ 4.1-4.2 weeks, over 6 months; Figure 14c).

Of those eels transplanted, 2 (18%) from site 6 and 2 (10%) from site 7 were recaptured downstream at their respective initial tagging site. One of these eels (site 6) was recaptured in November 1996, while the remaining 3 were recaptured in June 1997. All four eels were within 22-31cm long.

Although mortality rates were not estimated, only 8 tagged eels were found dead (2 in 1995, 6 in 1996). All of these had died within 1 m of the site of release and all occurred during the period of warmest water temperature (July, August). One potted eel (48 cm) collected for parasite analysis had a tag (from a 20 cm long eel) in its stomach, but no flesh.

3.2 Parasites Found

A total of 11 species of metazoan parasites from eels were identified, of which, 6 were **specialists** : *Pseudodactylogyrus anguillae* (Monogenea, gills); *Crepidostomum brevivitellum* (Digenea, intestine); *Proteocephalus macrocephalus* and *Bothriocephalus claviceps* (Cestoidea, intestine); *Paraquimperia tenerrima* (Nematoda, intestine) and *Ergasilus celestis* (Copepoda, gills); while 5 were **generalists**: *Azygia longa* (Digenea, stomach); *Eustrongylides* sp. (Nematoda, encysted in visceral mesentary); *Echinorhynchus salmonis, Neoechinorhynchus rutili* and *Pomphorhynchus bulbocolli* (Acanthocephala, intestine). The parasites *Eustrongylides sp., E. salmonis* and *N. rutili* were rare (< 1.0% of entire sample) and restricted to large eels (>40 cm) caught in pots.

The adult copepod (*E. celestis*) and adult monogene (*P. anguillae*) are gill parasites with monoxenous life cycles. The others have heteroxenous life cycles and, except *Eustrongylides* (found as larvae encysted in visceral mesentary) were found at various stages of maturity, in the intestine or stomach (*A. longa*). Metazoan parasites were absent from the urinary bladder, swimbladder, liver, gallbladder, muscle or skin. Some eels (25% of those less than 20cm) had specimens of *P. bulbocolli* that had bored through the intestinal wall and were in various stages of being lysed and encapsulated by a granulomatous tissue response; these parasites were not included in statistical analyses. All the above parasites are **autogenic** (completing their entire life cycle in water), with the exception of *Eustrongylides* sp.; it matures in birds and is considered **allogenic**. Appendix D outlines the life cycle of each of these metazoan parasites.

3.3 Parasite Infracommunity

Species Richness

The total prevalence of eels infested with intestinal helminths was similar over both sampling years (43.6% in 1995; 48.3% in 1996). The total prevalence of parasitized eels (including gill parasites) was also similar over both years (56.6% in 1995; 57.8% in 1996). The majority of eels harboured 0 (42-56 %) or 1 parasite species (30-36%) (Figure 15 a; b). The maximum species richness of the intestinal helminth infracommunity was 6 (0.09% of all eels in 1996) and the maximum species richness of the metazoan parasite assemblage (including gill parasites) was 7 (0.09% of all eels in 1996). Few eels collected (< 10%) had more than 3 species of metazoan parasites.

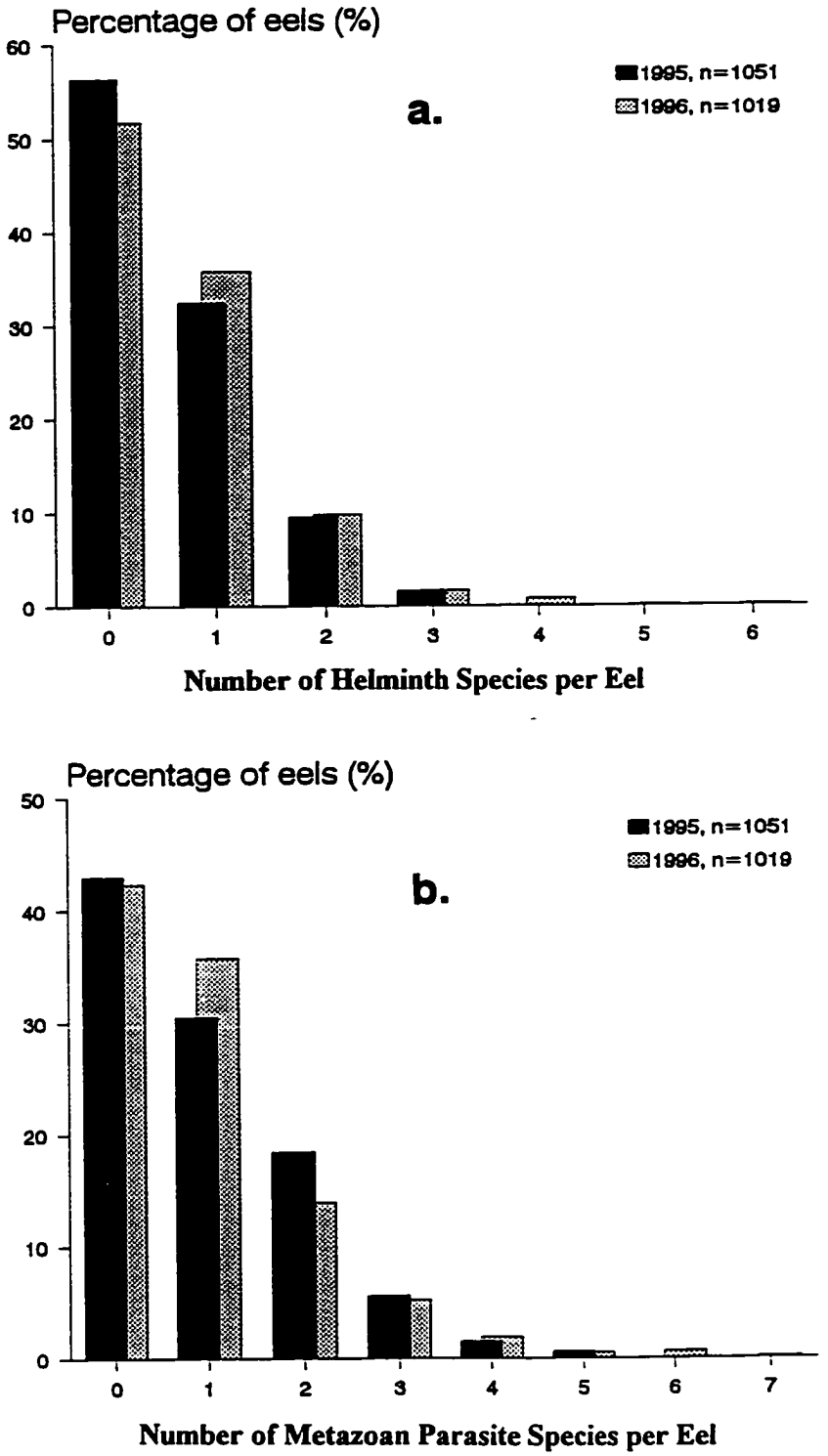


Figure 15. Frequency distribution (%) of the: (a.) number of different intestinal helminth species and (b.) number of different metazoan parasite species per eel during 1995 and 1996.

Throughout 1995 and 1996, patterns of helminth infracommunity richness and eel size were consistent. The percentage of eels with more than one intestinal helminth species ($\leq$ 15%) was very similar for each eel length class up to 35 cm, after which, each successive length class had an increase in the percentage of eels with > 1 species (~ 20-50%; Figure 16a). Eels greater than 45 cm had the highest percentage (~ 15-30%) of intestinal helminth infracommunities with species richness of 3 or greater and had the lowest percentage (~ 25%) of eels with no intestinal helminths (Figure 16a).

The frequency distribution of the parasite assemblage per eel was characterized by the same patterns. There was annual consistency and an increase in percentage of eels parasitized by > 1 species with each increasing eel length class (Figure 16b). The main difference in this frequency distribution was the greater decrease in the percentage of 'parasite-free' eels as length increased; less than 5 % of all eels greater than 45 cm had no parasites (Figure 16b). If eels (>45 cm) lacked a helminth intestinal parasite, most (~ 95%) would have at least one species of gill parasite.

Annual mean richness of the intestinal helminth infracommunity was positively correlated with eel length class ($r = 0.306$, $p < 0.001$). Annual mean ($\pm$ s.e.) richness was significantly greater (ANOVA; $p < 0.001$) in eels 45+ cm (1.90 $\pm$ 0.19 helminth species/eel in 1995; 2.13 $\pm$ 0.25 helminth species/eel in 1996) than in eels up to 40 cm (~ 1.0-1.6 helminth species/eel; Figure 17a). Eels of 30-45 cm had a significantly larger (ANOVA; $p < 0.05$) mean infracommunity richness (~ 1.3-1.6 helminth species/eel) than those up to 20 cm (~ 1.0-1.2 helminth spp/eel). The annual mean ($\pm$ s.e.) helminth infracommunity population (number of individuals/eel) increased with increasing eel length and was similar

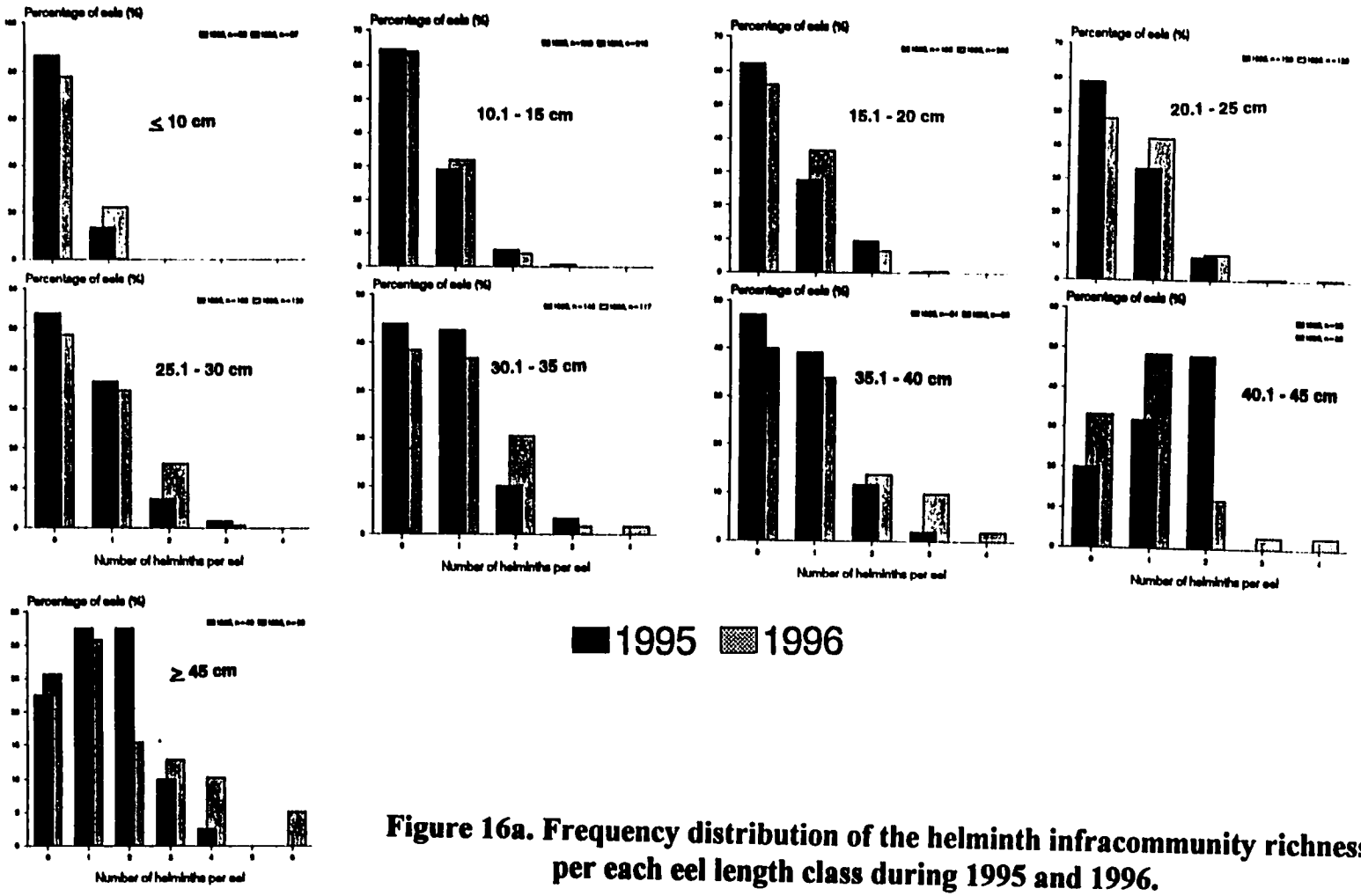


Figure 16a. Frequency distribution of the helminth infracommunity richness per each eel length class during 1995 and 1996.

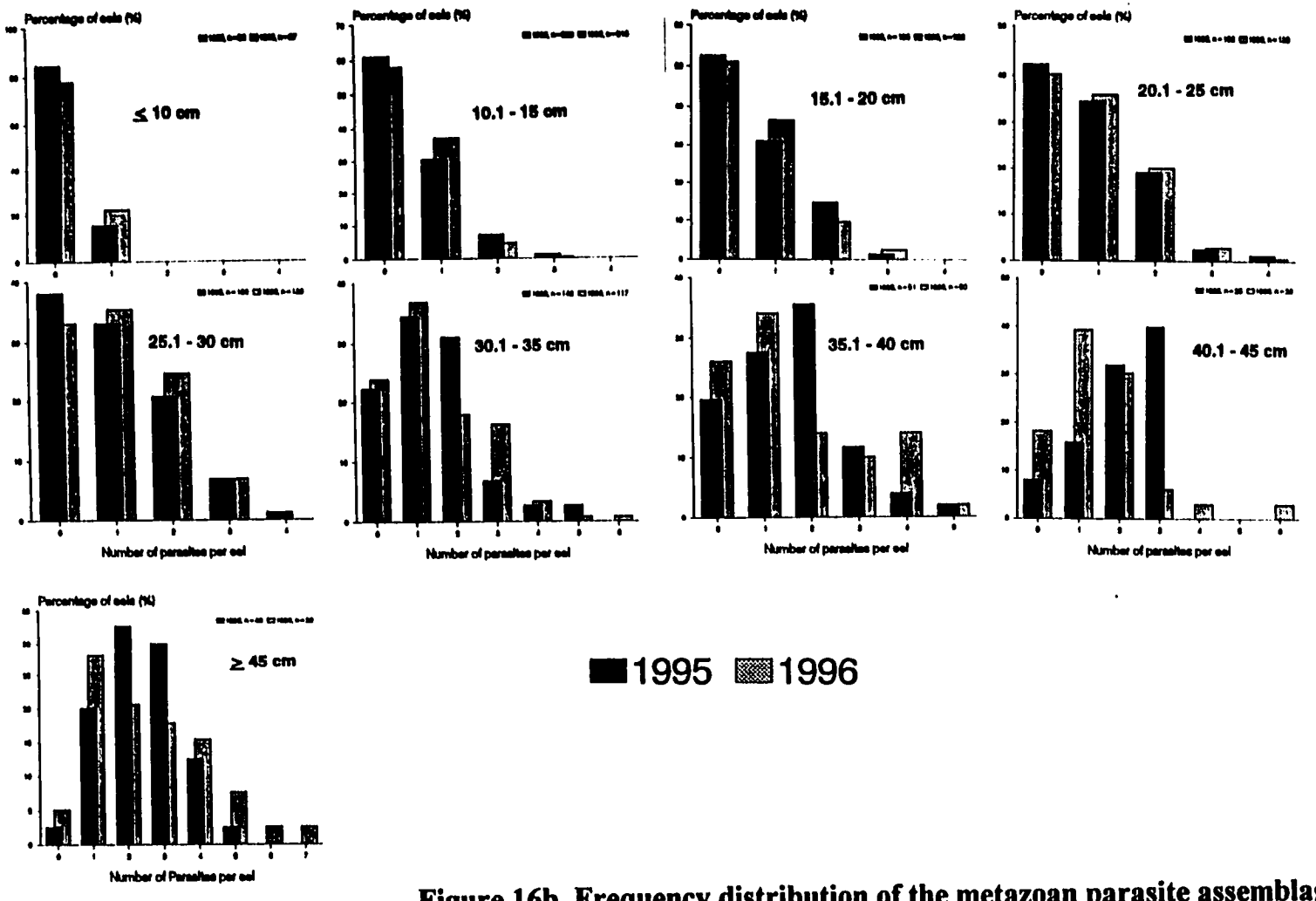


Figure 16b. Frequency distribution of the metazoan parasite assemblage richness per each length class during 1995 and 1996.

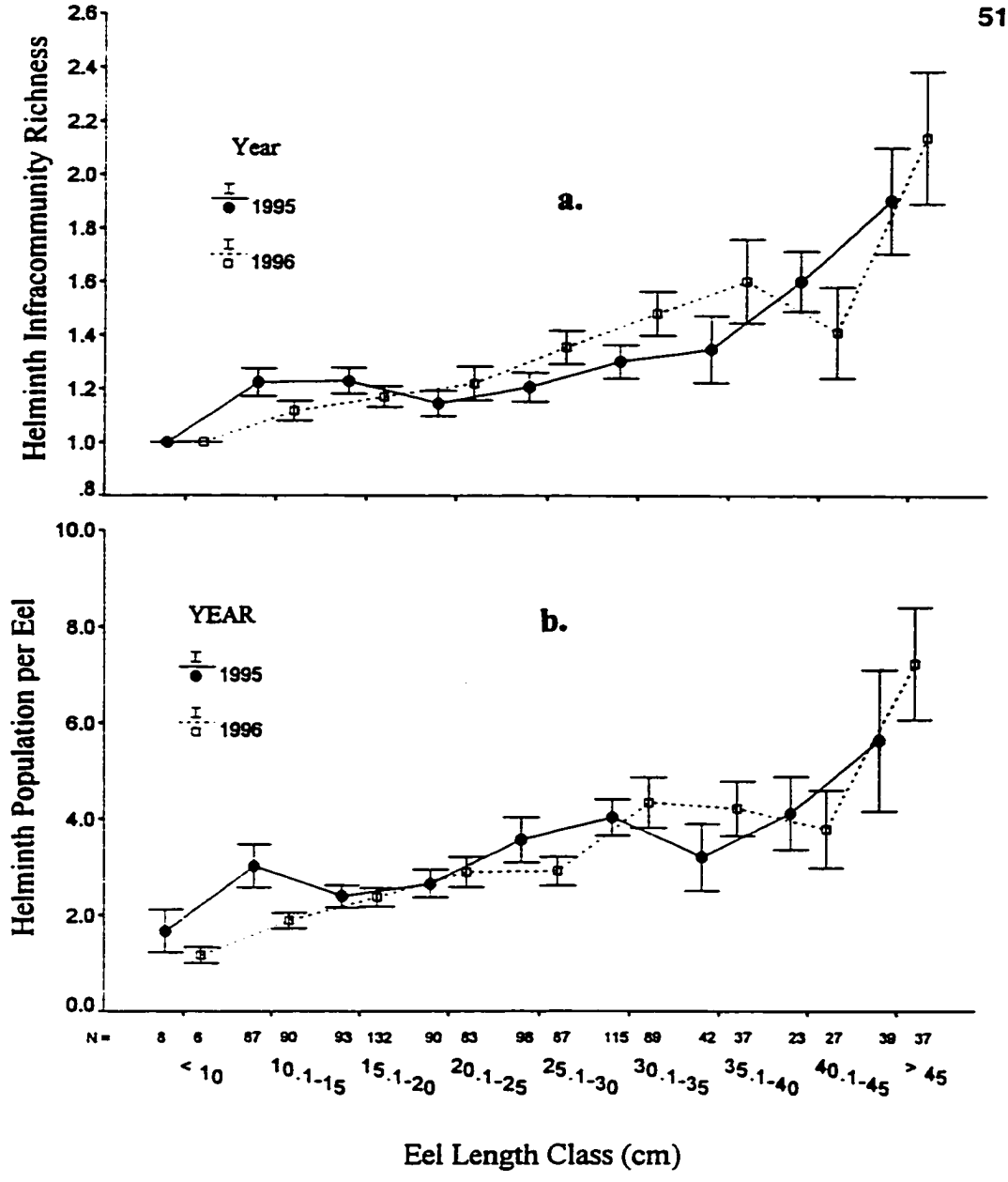


Figure 17. Annual mean (± s.e.): (a.) helminth infracommunity richness and (b.) helminth infracommunity population per eel length class.

from 1995 to 1996 (Figure 17b). In 1995, eels 45+ cm had significantly higher (ANOVA; $p < 0.002$) mean ($\pm$ s.e.) helminth populations (5.61 ± 1.47 helminths/eel) than those eels up to 25cm (~ 1.6-2.6 helminths/eel); however, in 1996, eels 45+ cm had significantly higher (ANOVA; $p < 0.001$) mean ($\pm$s.e.) helminth populations (7.20 ± 1.16 helminths/eel) than all other eel length classes.

The same positive correlation was evident for annual mean richness of the parasite assemblage per eel and eel length class ($r = 0.418$, $p < 0.001$). Similar consistency from 1995 to 1996 and similar trends existed, but mean parasite richness per eel was slightly larger (max. 2.5-2.7 parasite species/eel; Figure 18a). Eels 30 cm or larger had a mean species richness (~1.85-2.7 parasite species/eel) significantly greater (ANOVA; $p < 0.001$) than that in all smaller length classes (~ 1.0-1.5 parasite species/eel; Figure 18a). Eels greater than 30 cm had significantly higher (ANOVA; $p < 0.001$) annual mean parasite populations (~12.5-21.2 parasites/eel) than all smaller eels (Figure 18b). Note that the mean helminth infracommunity population per eel was not significantly different from 1995 to 1996, but the mean parasite assemblage population per eel was less (t - test, $p < 0.05$) in 1996 than in 1995, yet the same trend of higher mean parasite populations in larger eels was evident.

To account for variability among habitats, similar plots of : (i) helminth infracommunity richness; (ii) intestinal helminth population (iii) parasite assemblage richness and (iv) parasite population per eel length class were constructed for each sample site. Similar trends of annual consistency and increasing species richness and mean population with increasing eel length class existed, with some exceptions. At the most

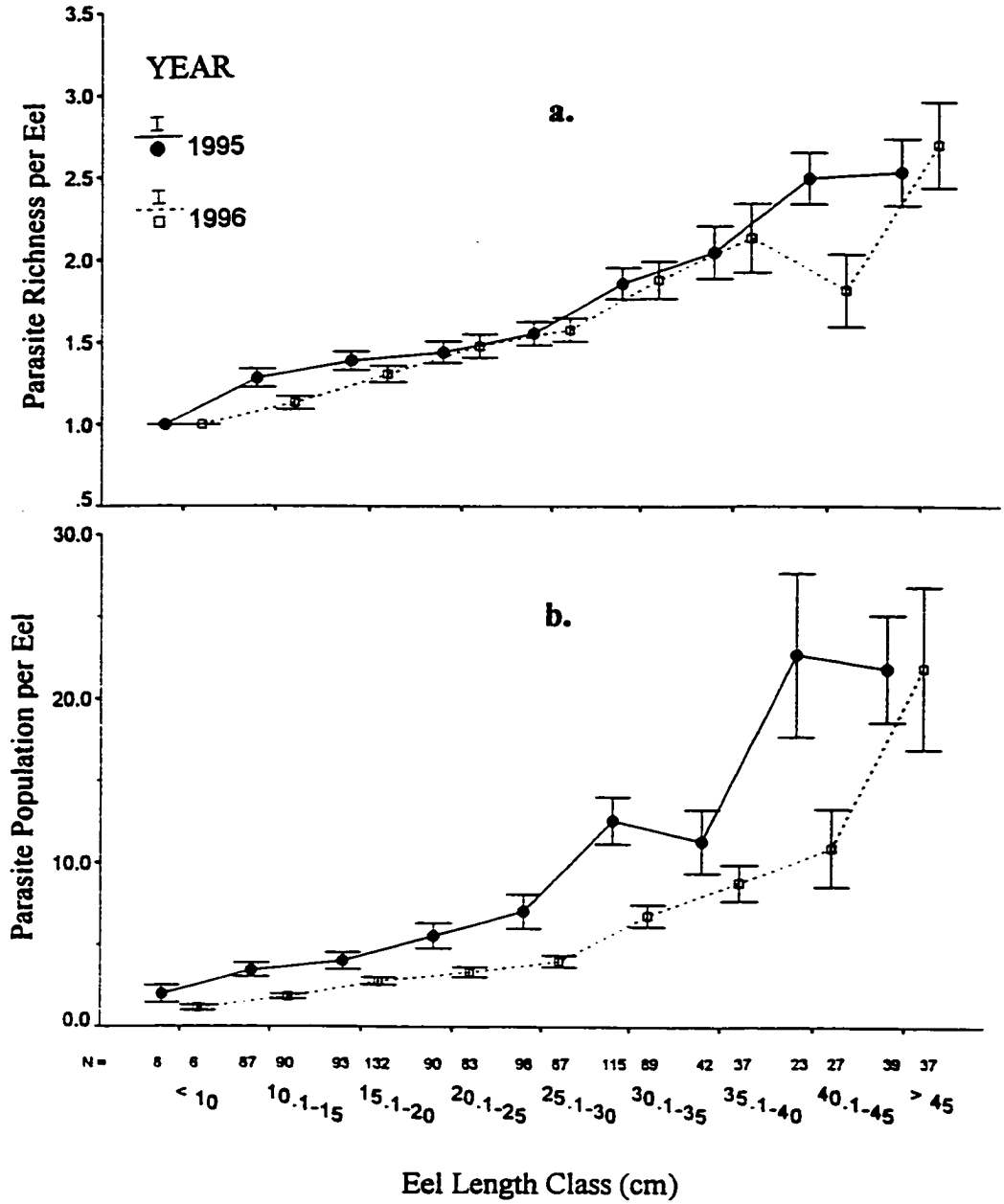


Figure 18. Annual mean (± s.e.): (a.) metazoan parasite assemblage richness and (b.) metazoan parasite population per eel length class.

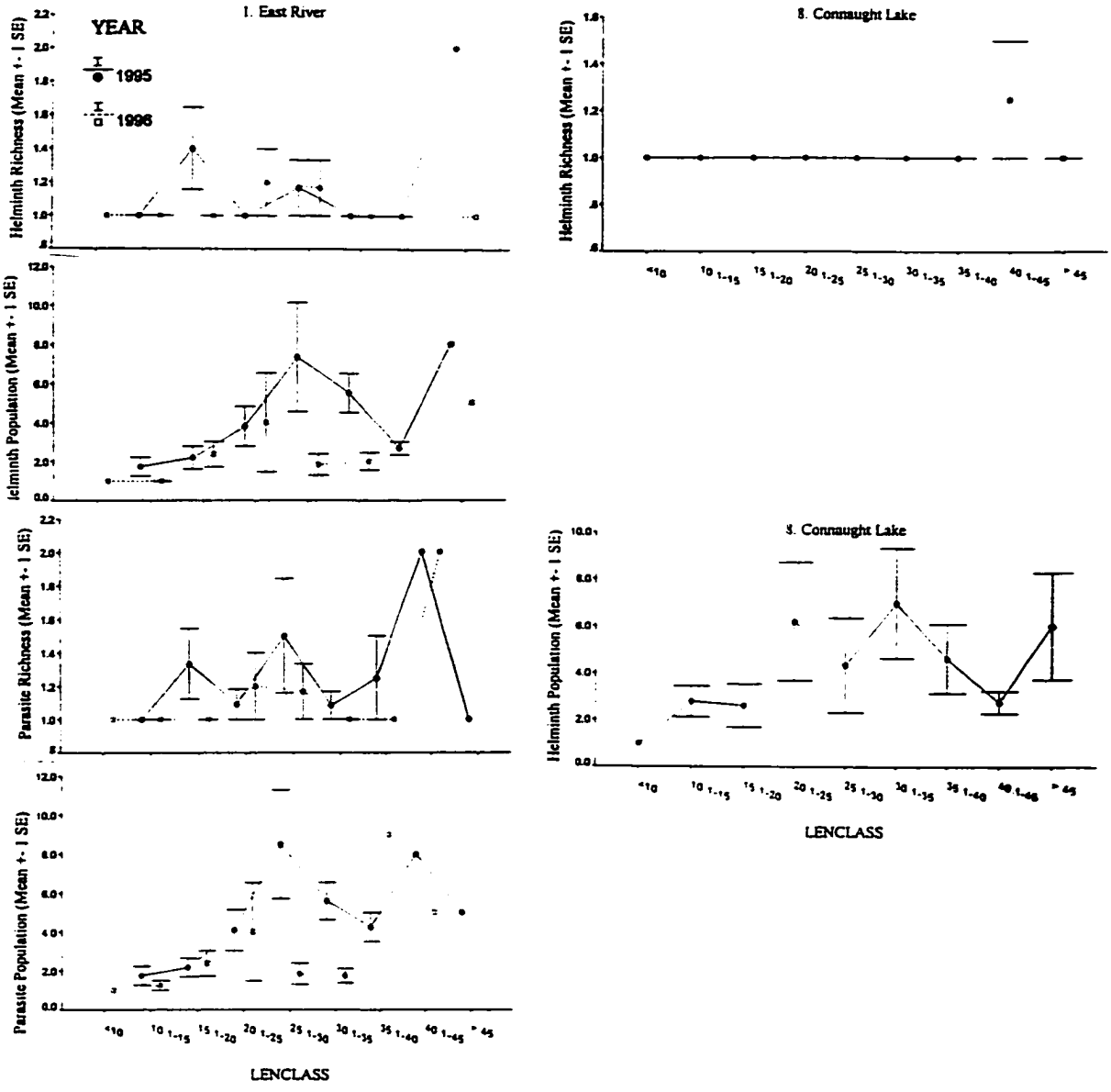


Figure 19a. Annual mean (± s.e.) helminth infracommunity richness, helminth infracommunity population, metazoan parasite assemblage richness and metazoan parasite assemblage population per eel length class at sites 1 (East River) and 8 (Connaught). (No plots of parasite assemblage richness or population were constructed for Connaught as no gill parasites were found.)

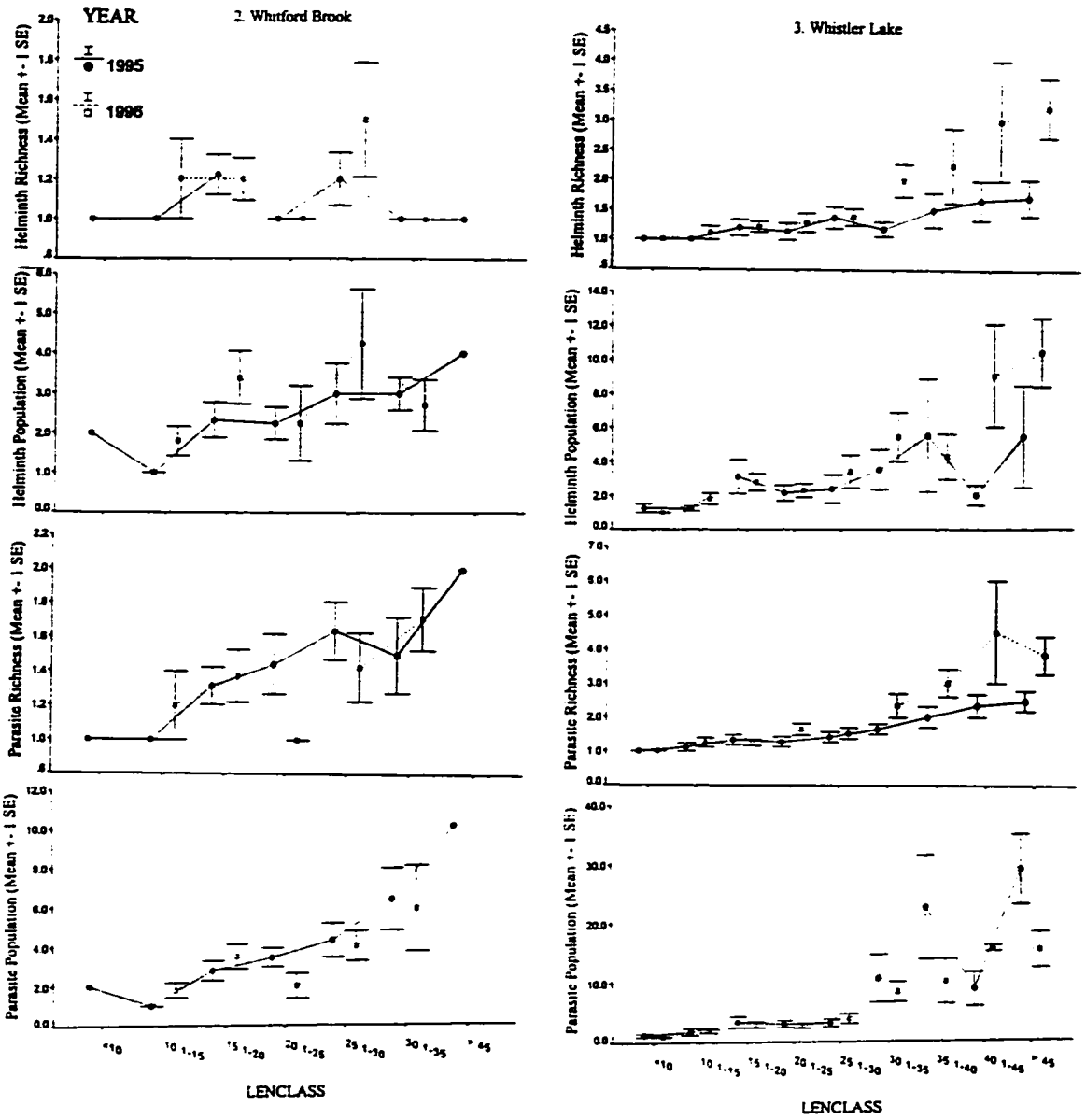


Figure 19b. Annual mean (± s.e.) helminth infracommunity richness, helminth infracommunity population, metazoan parasite assemblage richness and metazoan parasite assemblage population per eel length class at sites 2 (Whitford Brook) and 3 (Whistler Lake).

acidic sites (1, 2 & 8), there were no significant differences (ANOVA; $p > 0.50$) in helminth infracommunity richness, helminth population, parasite assemblage richness or parasite population among each eel length class (Figure 19a; b). Both species of gill parasites were absent from site 8, while both species of Digenea and the acanthocephalan were absent from sites 8 and 1 and rare at site 2. Eels from these 3 sites had the lowest helminth infracommunity richness and parasite assemblage richness of all sample sites. Among the other sample sites of greater pH (sites 3-7), the trends of annual consistency and increasing species richness and population with increasing eel length were common (Figure 19b-d).

When comparing mean helminth infracommunity and parasite assemblage richness of a common eel length class among different sample sites, there were no significant differences (ANOVA; $p > 0.50$), regardless of where the eels originated. This pattern was consistent for each eel length class to 35 cm; after which, eels from the sites of highest pH (sites 3-7) had significantly higher (ANOVA; $p < 0.001$) mean values of helminth infracommunity and parasite assemblage richness. The total annual mean ($\pm$ s.e.) helminth infracommunity richness was highest (ANOVA; $p < 0.001$) in eels collected in pots (1.79 $\pm$ 0.16 helminth spp/eel in 1995; 2.14 $\pm$ 0.18 helminth spp/eel in 1996), and lowest in eels from sites 8 and 1 (~ 1.10-1.17 helminths per eel; Figure 20a). Annual mean helminth infracommunity population per eel was highest (ANOVA; $p < 0.001$) in potted eels (~ 5.1-6.0 helminths/eel) and in eels from sites 1 and 8 (~ 4.2-4.5 helminths/eel), with little or no difference among remaining sample sites (Figure 20b).

The same patterns existed for the total mean parasite assemblage richness and

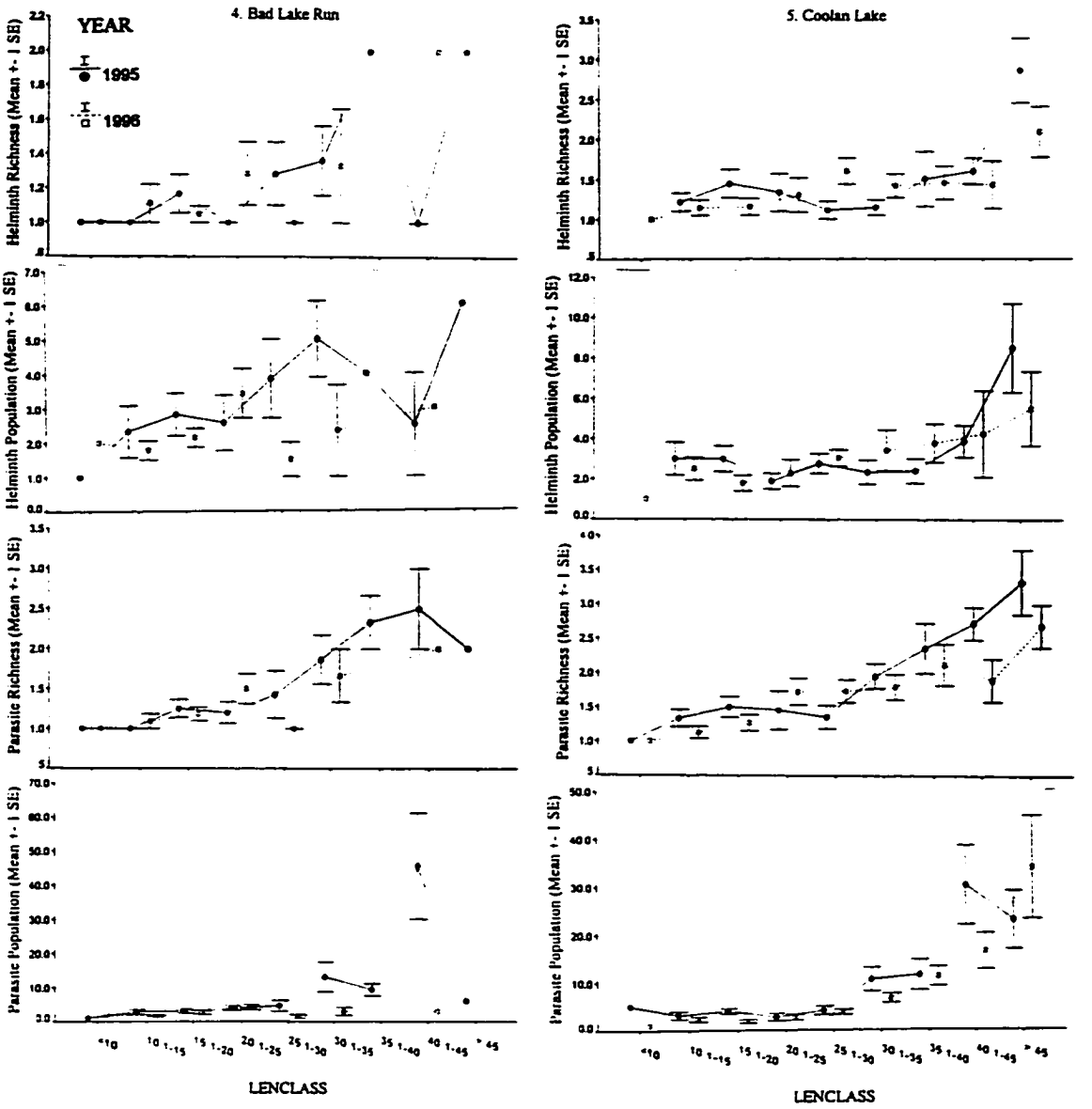


Figure 19c. Annual mean (± s.e.) helminth infracommunity richness, helminth infracommunity population, metazoan parasite assemblage richness and metazoan parasite assemblage population per eel length class at sites 4 (Bad Lake Run) and 5 (Coolan Lake).

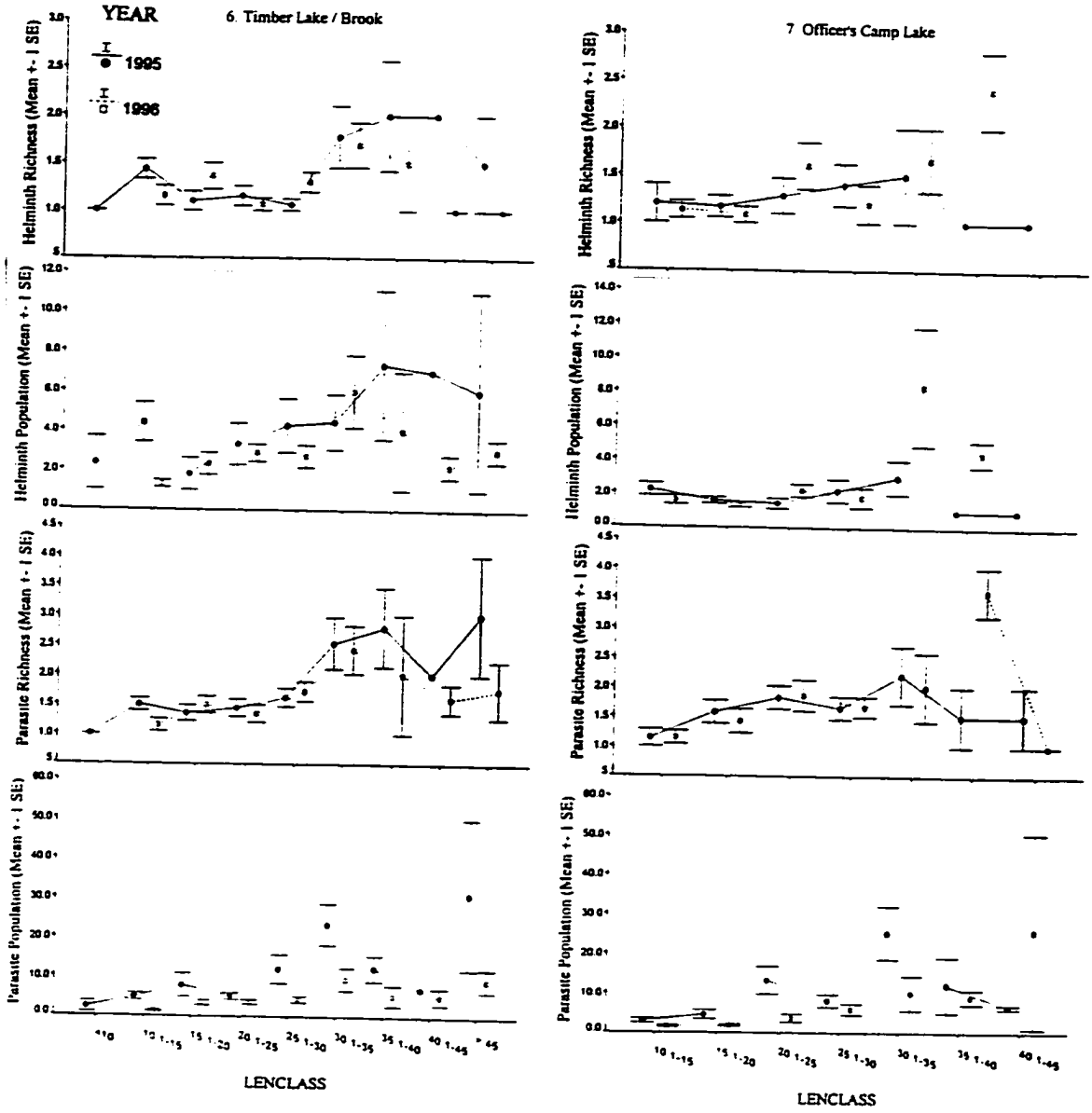


Figure 19d. Annual mean (± s.e.) helminth infracommunity richness, helminth infracommunity population, metazoan parasite assemblage richness and metazoan parasite assemblage population per eel length class at sites 6 (Timber Lake) and 7 (Officer's Camp Lake).

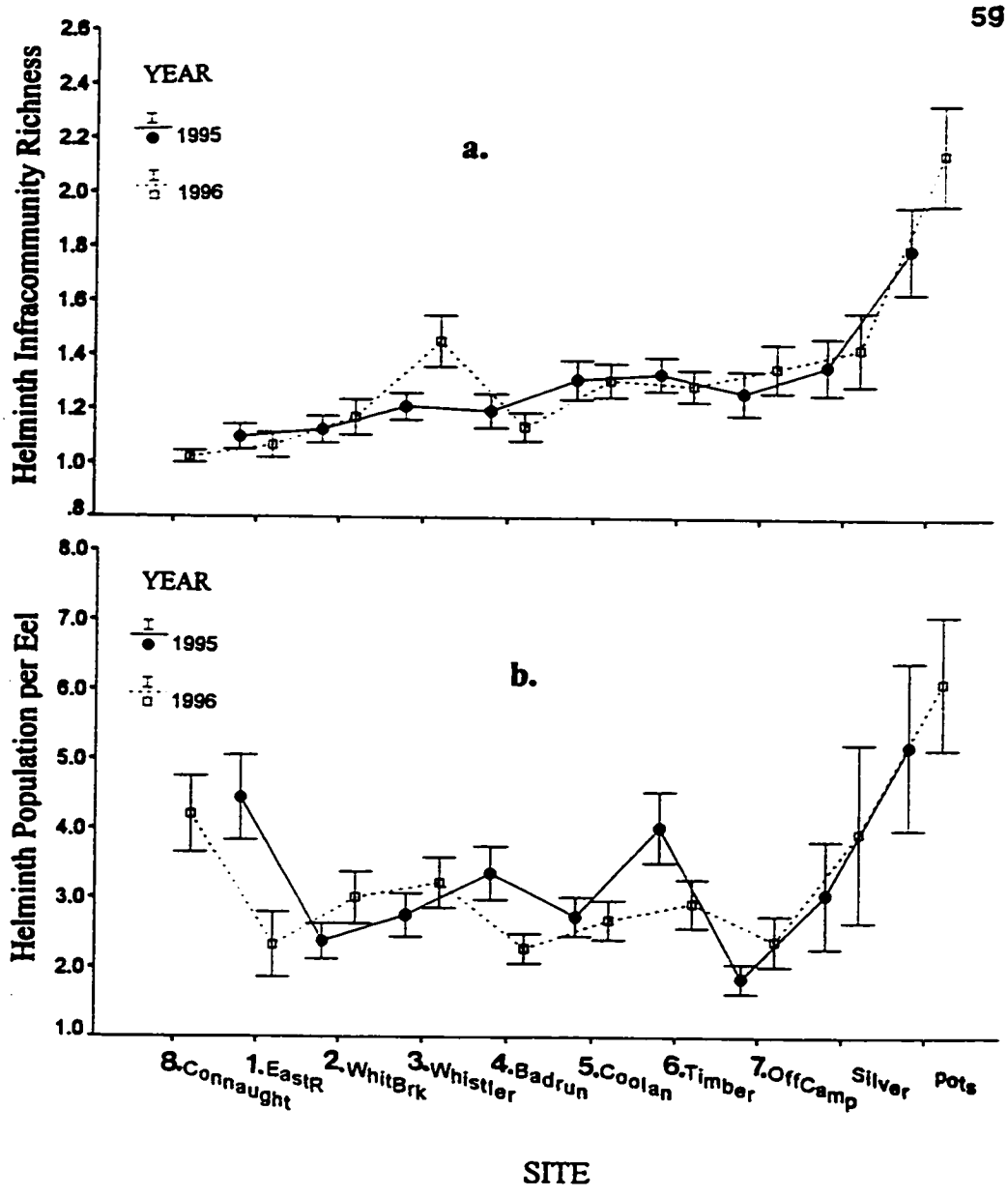


Figure 20. Total annual mean (± s.e.): (a.) helminth infracommunity richness and (b.) helminth infracommunity population at each sample site.

population per sample site. The annual mean (± s.e.) assemblage richness was highest (ANOVA; $p < 0.001$) in potted eels (2.65 ± 0.16 parasite spp/eel in 1995; 2.70 ± 0.20 parasite spp/eel in 1996), while eels from sites 3, 5-7 had annual mean richness values (~ 1.55-1.69 parasite spp/eel) significantly greater (ANOVA; $p < 0.001$) than those from eels collected at sites 1 and 8 (Figure 21a). Annual mean parasite population per eel was highest (ANOVA; $p < 0.001$) in potted eels (~ 23-25 parasites/eel) and lowest in eels from sites 8, 1-2 (~ 2.1-4.7 parasites/eel) , with little or no difference among remaining sample sites (Figure 21b). Overall, mean parasite populations per eel in 1995 were higher than those in 1996 at each sample site, excluding potted and silver eels.

Interestingly, silver eels (90% collected from site 1) had significantly higher (ANOVA; $p < 0.001$) annual mean helminth infracommunity and parasite assemblage species richness than yellow eels collected at site 1. These silver eels were often 'additionally' infested by digenes, which were absent from yellow eels at site 1 throughout 1995 and 1996. In addition, there was often a high prevalence and mean abundance of both gill parasite species among silver eels - a combination never observed among samples of yellow eels at site 1.

Composition

The helminth infracommunity could be dominated (numerically) by any one of the 6 'common' intestinal helminths. However, they were most often dominated by the nematode, *Paraquimperia tenerrima* (51.2% in 1995; 49.5% in 1996), followed by either: *Pomphorhynchus bulbocolli* (12.3% in 1995; 15.4% in 1996); *Crepidostomum*

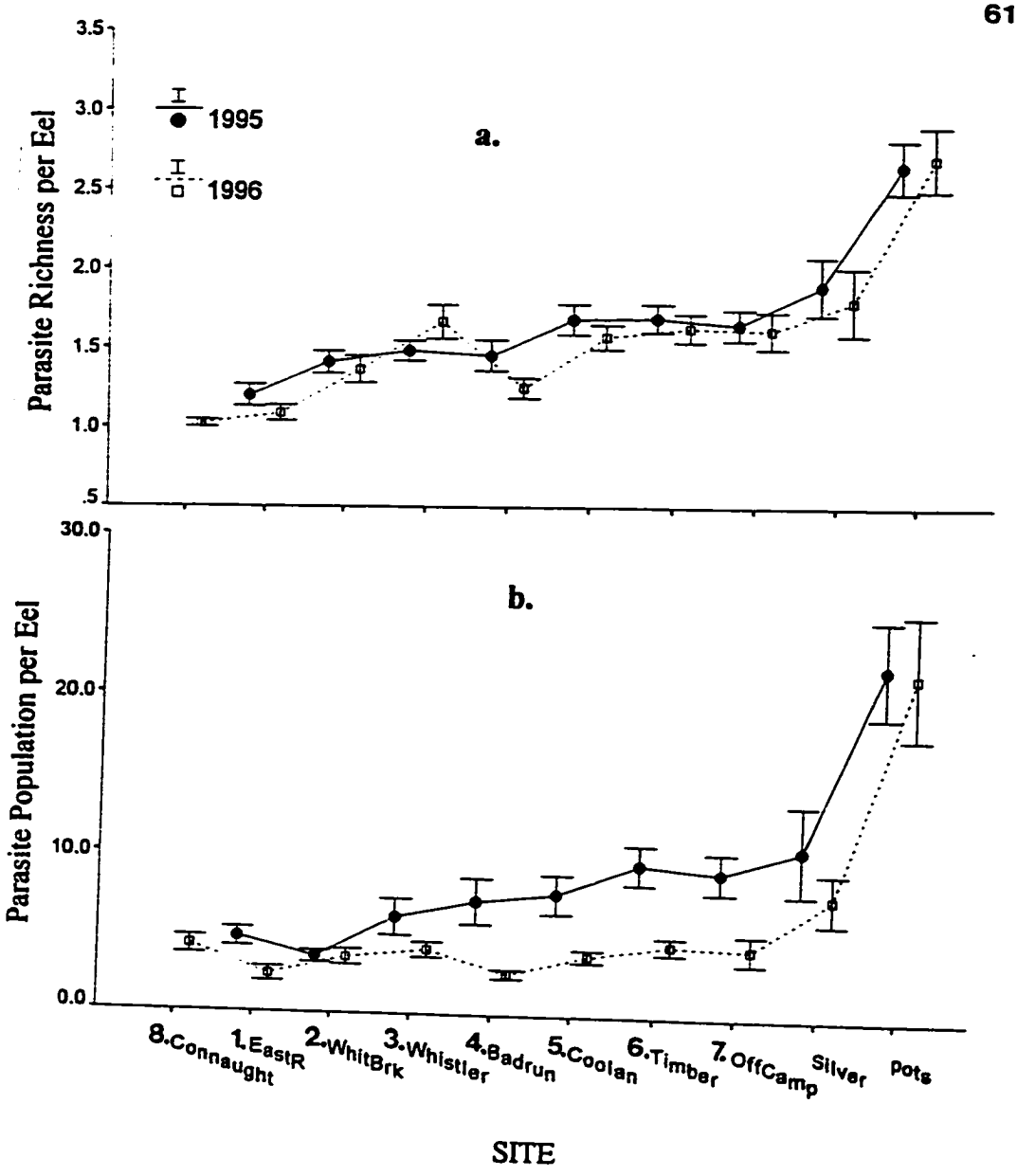


Figure 21. Total annual mean (± s.e.): (a.) metazoan parasite assemblage richness and(b.) metazoan parasite population per eel at each sample site.

brevivitellum (13.5% in 1995; 15.4% in 1996) or *Azygia longa* (13.5% in 1995; 9.9% in 1996). Both species of cestode were rare and dominated a similar percentage of infracommunities: (i) *Bothriocephalus claviceps* - 6.6% in 1995 and 1996 (ii) *Proteocephalus macrocephalus* - 2.7% in 1995; 3.1% in 1996. The uncommon helminths *Eustrongylides* sp., *Neoechinorhynchus rutili* dominated less than 5% of the infracommunities of large eels (> 40cm).

The percentage of infracommunities dominated by either *P. tenerrima* or *P. bulbocolli* decreased with increasing eel length from year to year (Figure 22a). The smallest eels (< 10 cm) had the highest percentage of infracommunities dominated by *P. tenerrima* or *P. bulbocolli* (~75-80% and ~27-35% respectively); while the largest eels (>40 cm) had the lowest percentage of infracommunities dominated by *P. tenerrima* or *P. bulbocolli* (~15-33% and < 10% respectively; Figure 22a). The percentage of infracommunities dominated by digenes (*C. brevivitellum*, *A. longa*) or cestodes (*B. claviceps*, *P. macrocephalus*) increased with increasing eel length from year to year (Figure 22a). Overall, in larger eels, each species had an almost equal probability of dominating the infracommunity, while in smaller eels, usually *P. tenerrima* or *P. bulbocolli* had the greatest probability of dominating the infracommunity.

Differences in infracommunity composition were also evident among the sample sites. The helminth infracommunities of eels from the most acidic sites (1 & 8) were only dominated by one of three species, usually *P. tenerrima* (~77-90%) which dominated a higher percentage of infracommunities at sites 1,2 and 8 than any other site during 1995 and 1996 (Figure 22b). The helminth infracommunities of eels from the site of highest pH

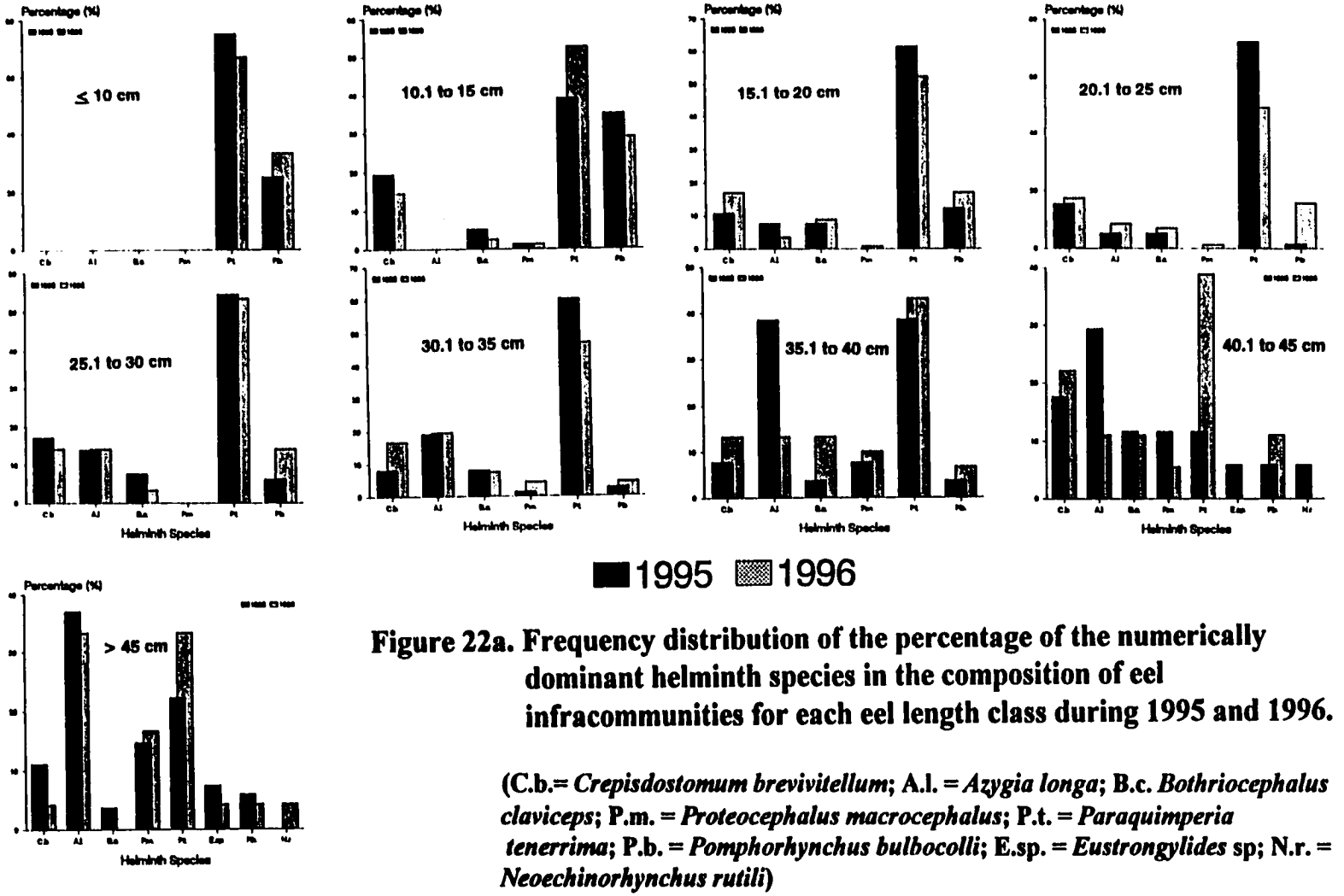


Figure 22a. Frequency distribution of the percentage of the numerically dominant helminth species in the composition of eel infracommunities for each eel length class during 1995 and 1996.

(C.b.= *Crepisdostomum brevivitellum*; A.l. = *Azygia longa*; B.c. *Bothriocephalus claviceps*; P.m. = *Proteocephalus macrocephalus*; P.t. = *Paraquimperia tenerrima*; P.b. = *Pomphorhynchus bulbocolli*; E.sp. = *Eustrongylides* sp; N.r. = *Neoechinorhynchus rutili*)

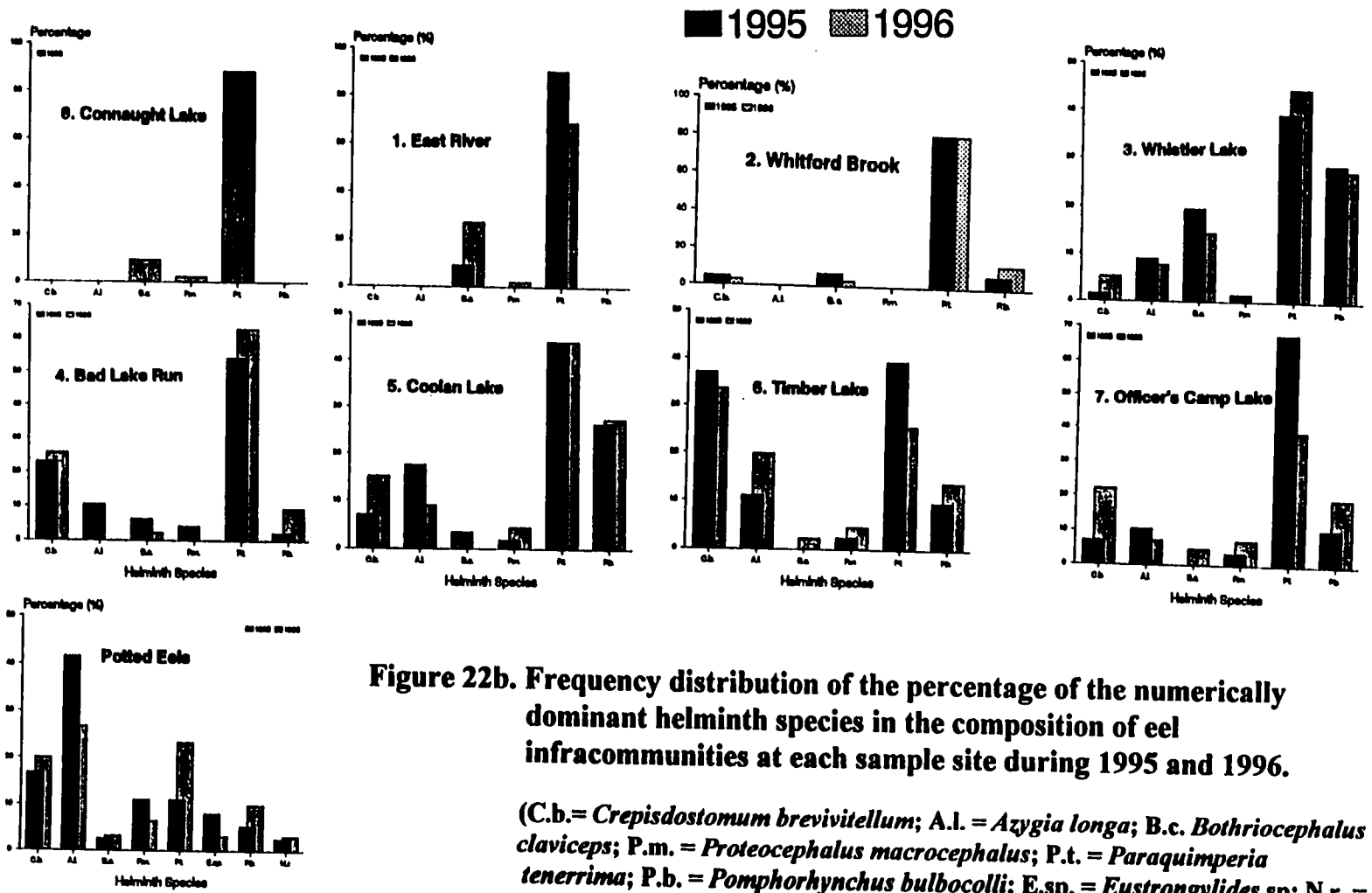


Figure 22b. Frequency distribution of the percentage of the numerically dominant helminth species in the composition of eel infracommunities at each sample site during 1995 and 1996.

(C.b.= *Crepisdostomum brevivitellum*; A.l. = *Azygia longa*; B.c. *Bothriocephalus claviceps*; P.m. = *Proteocephalus macrocephalus*; P.t. = *Paraquimperia tenerrima*; P.b. = *Pomphorhynchus bulbocolli*; E.sp. = *Eustrongylides* sp; N.r. = *Neoechinorhynchus rutili*)

(site 6) had the highest percentage of infracommunities dominated by digenes (~ 35-38% for *C. brevivitellum*; ~ 11-20% for *A. longa*; Figure 22b). Potted eels had similar high percentages for digenes, but the values were reversed (~ 16-20% for *C. brevivitellum*; ~ 33-38% for *A. longa*). These potted eels (a combination from the lacustrine habitat of sites 3 & 5) had more helminth species 'available' to dominate the intestinal infracommunity (8 vs. 6 spp.) than electrofished eels from the same sites. Additionally, these potted eels had a higher percentage of digenes (~ 16-38% vs. 2-15%) and a lower percentage of nematodes (~ 8-24% vs. 38-45%) dominating the infra-community than electrofished eels from the same sites (Figure 22b).

Among eels infested with multiple helminth species, the percent occurrence of possible parasite combinations were not equal. In electrofished eels, the combinations of parasites from dissimilar feeding guilds (e.g. absorber and particle feeder) were most common (digene & nematode: 22.7% in 1995; 27.1% in 1996; cestode and nematode: 23.7% in 1995; 18.6% in 1996), while combinations of common taxa (cestode & cestode, nematode and nematode) and common feeding guild (acanthocephalan and cestode) were absent to rare (< 5%; Figure 23). Among potted eels, similar patterns existed, but the percent occurrence of parasites from common taxa and common feeding guilds was higher (Figure 23). There were no significant differences in tests of association (based on presence/absence data) of intestinal helminth species among potted eels during 1995 and 1996 (W statistic = 23.80 in 1995; 22.41 in 1996). However, the intestinal helminth species of electrofished eels were overall negatively associated (Variance Ratio = 0.295 in 1995; 0.364 in 1996, W statistic = 121.64 in 1995; 167.47 in 1996). Individually, there

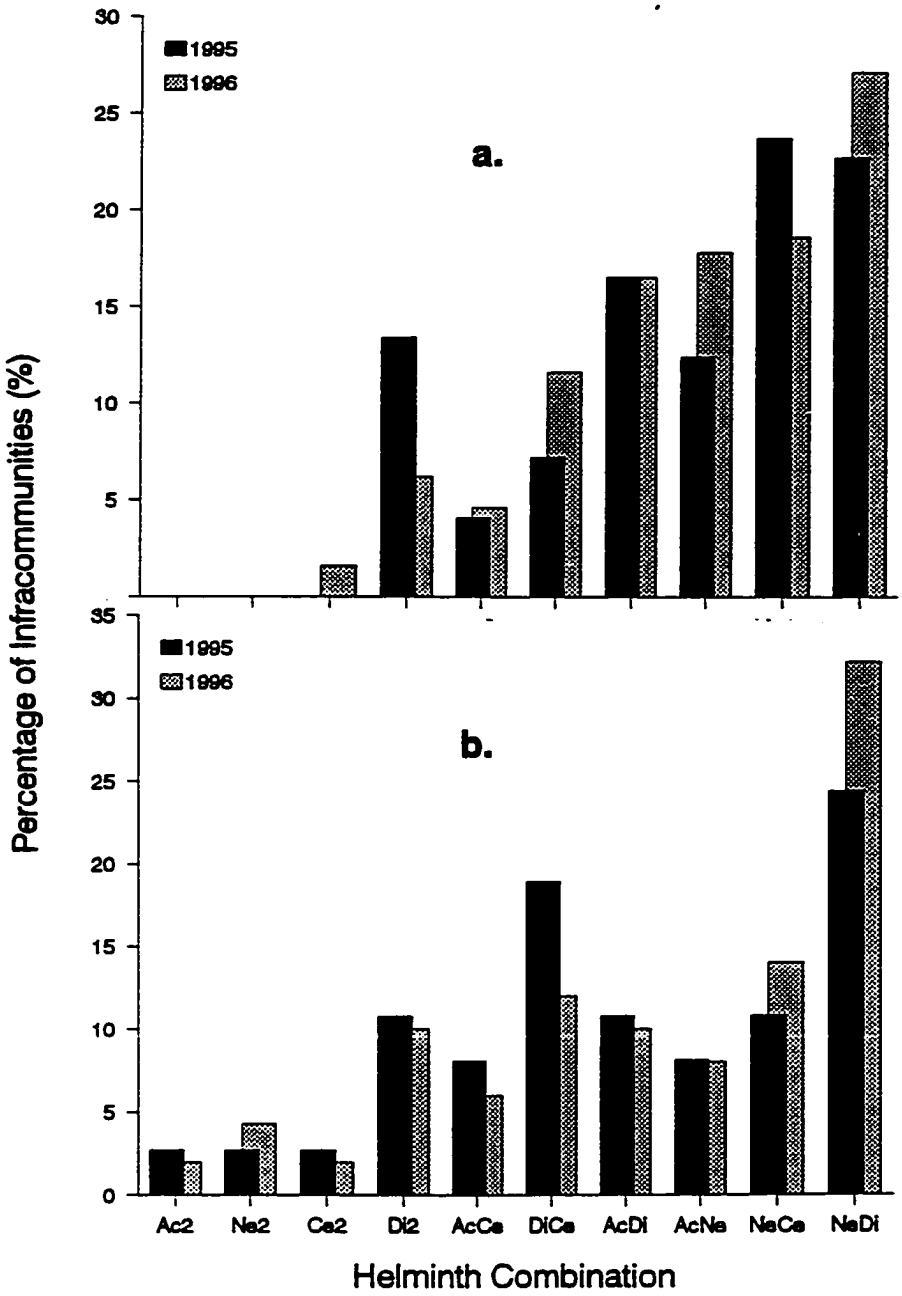


Figure 23. Percentage of helminth infracommunities with different combinations of intestinal helminths among: (a.) electrofished eels and (b.) potted eels during 1995 and 1996.

Ac2 = 2 sp of Acanthocephala
Ne2 = 2 sp of Nematoda
Ce2 = 2 sp of Cestoda
Di2 = 2 sp of Digenea
AcCe = Acanth & Cestode
DiCe = Digene & Cestode
AcDi = Acanth & Digene
AcNe = Acanth & Nematode
NeCe = Nematode & Cestode
NeDi = Nematode & Digene

was a negative association between all species pairs of *P. tenerrima* and each intestinal helminth species: *P. bulbocolli*, *A. longa*, *C. brevivitellum*, *B. claviceps* and *P. macrocephalus* ($\chi^2 \sim 3.90$-68.71) during 1995 and 1996. Additionally, values of species association indices (Ochiai, Dice and Jaccard) for these same species pairs were all less than 0.12, with over 80% less than 0.07.

There were no significant differences in covariance among helminth species abundances during 1995. However, in 1996, the abundances of *P. bulbocolli* and *P. macrocephalus* were positively correlated among potted and electrofished eels ($r = 0.578$, $r = 0.234$ respectively; $p < 0.01$). Furthermore, among electrofished eels, a significant positive correlation existed between the abundance of *P. bulbocolli* and *P. tenerrima* ($r = 0.234$; $p < 0.01$) while a significant negative correlation was found between the digenes *A. longa* and *C. brevivitellum* ($r = -0.123$; $p < 0.01$).

3.4 Parasite Component Community

Population Biology and Spatiotemporal Dynamics

The intestinal helminth, *Paraquimperia tenerrima*, had the highest prevalence of the entire sample (24% in 1995; 27.6% in 1996), followed by the copepod gill parasite, *Ergasilus celestis* (23.5% in 1995 and 1996; Figure 24). The gill monogene, *Pseudodactylogyrus anguillae*, had the next highest prevalence during 1995 (18.3%), but its prevalence dropped to 5.2% in 1996. It was the only parasite to show any significant difference in its abundance from 1995 to 1996. The remaining intestinal helminths had similar overall prevalences (< 10% in 1995 and 1996), with both species of cestode having

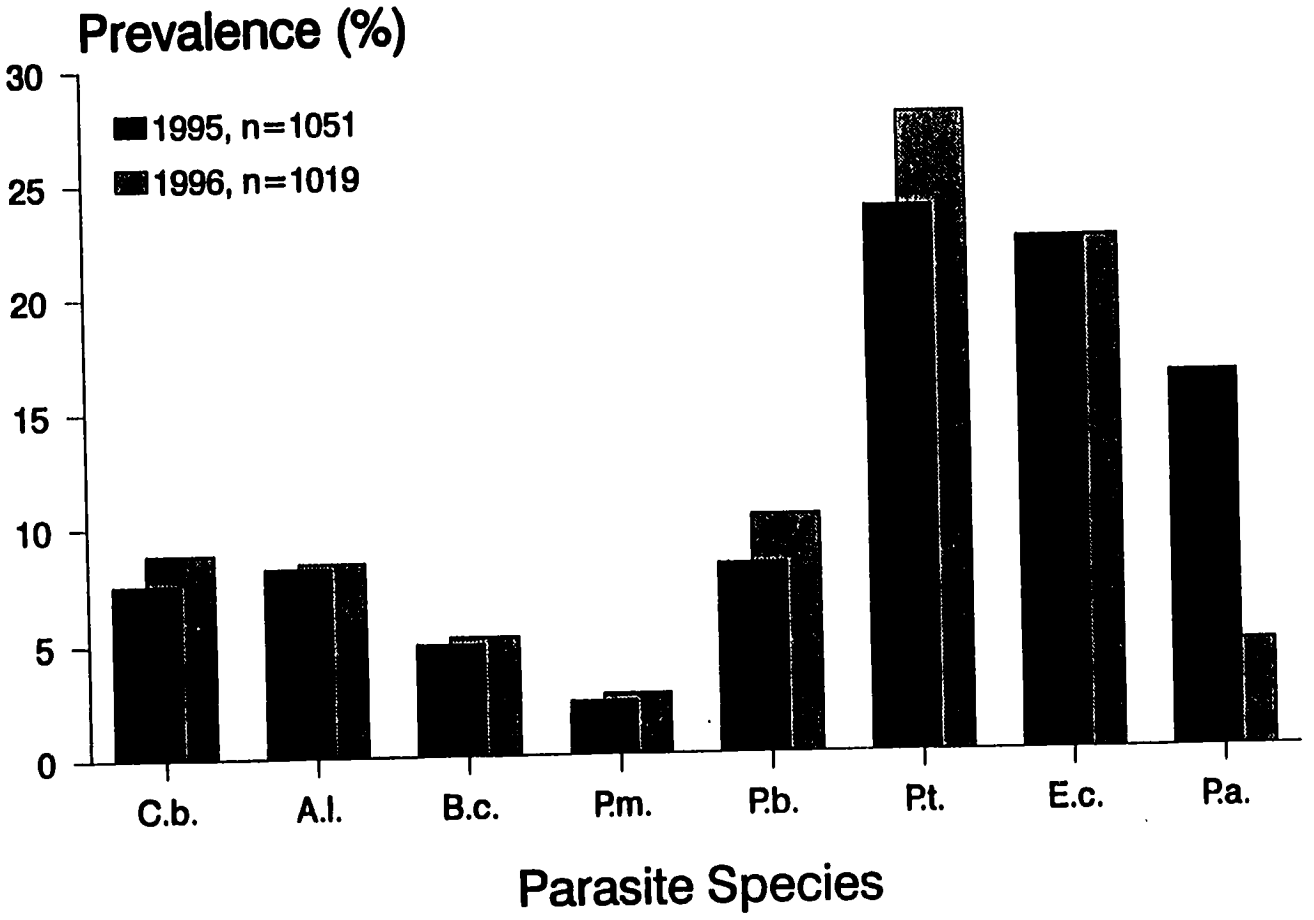


Figure 24. Total prevalence (%) of the 8 most common metazoan parasite species during 1995 and 1996. (C.b. = *Crepidostomum brevivitellum*, A.l. = *Azygia longa*, B.c. = *Bothriocephalus claviceps*, P.m. = *Proteocephalus macrocephalus*, P.b. = *Pomphorhynchus bulbocolli*, P.t. = *Paraquimperia tenerrima*, E.c. = *Ergasilus celestis*, P.a.= *Pseudodactylogyrus anguillae*).

the least (< 6.5%; Figure 24).

There were significant differences in prevalence and mean abundance of the 8 'common' parasites from site to site and among the different eel size classes. The digenes, *Azygia longa* and *Crepidostomum brevivitellum*, were absent from the sites of lowest pH (sites 8 and 1) throughout 1995 and 1996. The annual prevalence (%) and mean (± s.e.) abundance of *A. longa* were highest (G-test, $p < 0.05$; ANOVA; $p < 0.001$ respectively) in potted eels (42.9%, 1.42 ± 0.35 parasites/eel in 1995; 44.7%, 1.32 ± 0.33 parasites/eel in 1996) and silver eels (28.5%, 0.37 ± 0.11 parasites/eel in 1995; 26.9%, 0.58 ± 0.22 parasites/eel in 1996; Figure 25a). There were no significant differences in prevalence and mean abundance among all remaining sites were *A. longa* was found. Among those eels infested with *A. longa*, there was no significant difference in mean intensity among the various sample sites. As eel length increased, there was an increase in annual prevalence and mean abundance of *A. longa*, such that eels greater than 40 cm had a significantly higher (G-test, $p < 0.05$; ANOVA; $p < 0.05$) prevalence and mean abundance (respectively) than all smaller eels (Figure 25a). Among infested eels only, the annual mean intensity of *A. longa* was significantly greater (ANOVA; $p < 0.05$) in eels 45+ cm (3.73 ± 0.77 parasites/infested eel in 1995; 3.39 ± 0.64 parasites/infested eel in 1996) than that of eels less than 30 cm (~ 1.0-1.8 parasites/infested eel). From month to month, there were no significant differences in annual prevalence (Appendix B1), mean abundance or mean intensity of *A. longa*. Both gravid and sexually immature specimens could be found during any sampling month, but the ratio of gravid to immature specimens was highest during August - September.

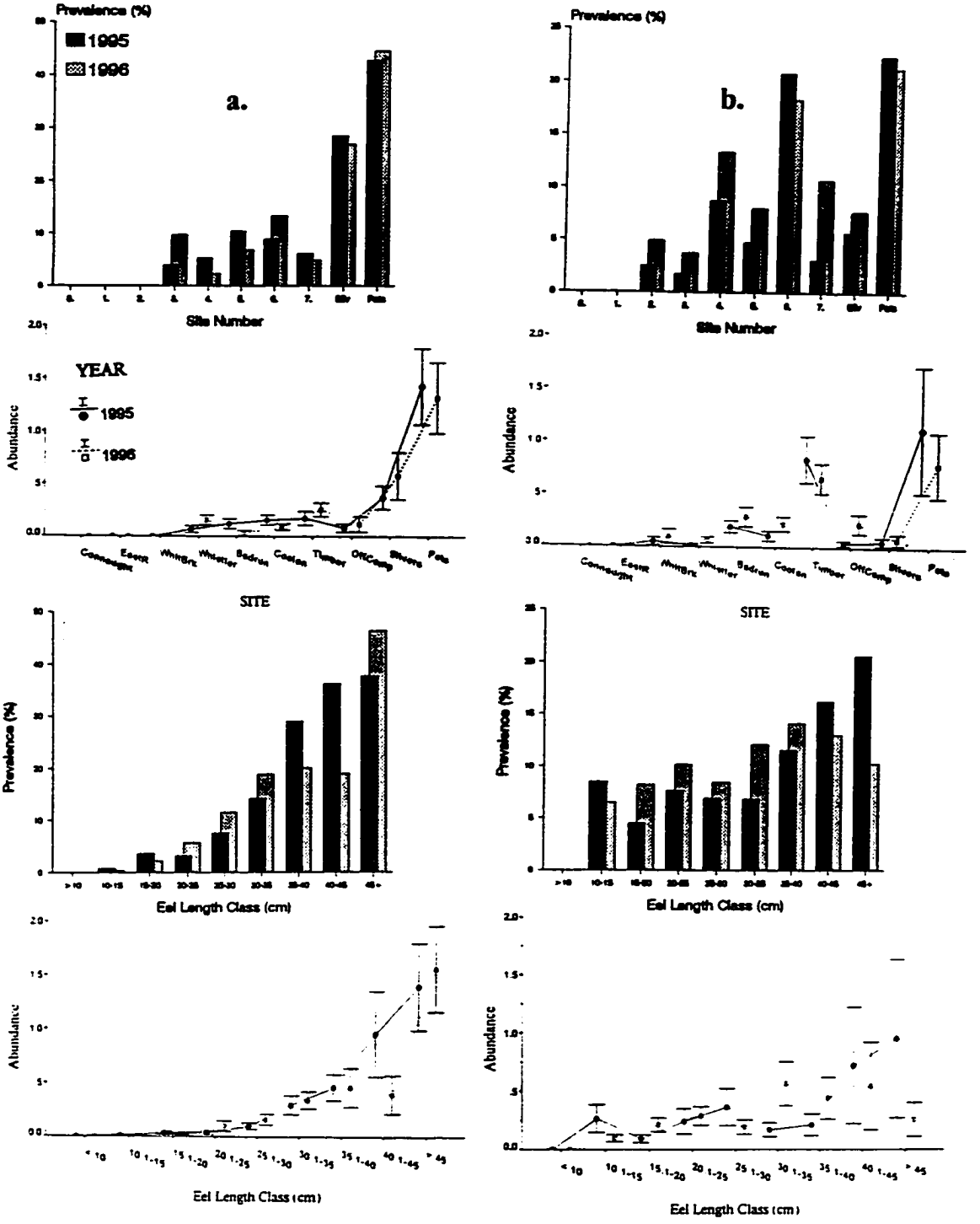


Figure 25. Annual prevalence (%) and mean (± s.e.) abundance of : (a.) *Azygia longa* and (b.) *Crepidostomum brevivitellum* at each sample site and for each eel length class during 1995 and 1996.

The annual prevalence (%) and mean (± s.e.) abundance of the second digene, *C. brevivitellum*, was highest in potted eels (22.4%, 1.12 ± 0.60 parasites/eel in 1995; 21.3%, 0.78 ± 0.31 parasites/eel in 1996), and in eels from the site of highest pH (site 6; 20.8%, 0.83 ± 0.22 parasites/eel in 1995; 18.3%, 0.66 ± 0.14 parasites/ eel in 1996; Figure 25b). Among infested eels only, there was no significant difference in annual mean intensity of *C. brevivitellum* among the sample sites or among the different eel length classes. There was no significant increase in annual mean abundance of *C. brevivitellum* with an increase in eel length, but the prevalence was highest in eels greater than 40 cm during 1995 (~ 16-20%; Figure 25b). From month to month, there were no significant differences in annual prevalence (Appendix B1), mean abundance or mean intensity of *C. brevivitellum*. Most immature specimens were found in October and the following May, and gravid forms were abundant in June and September.

During 1995, there were no significant differences in annual mean abundance of the cestode, *Bothriocephalus claviceps*, among the sample sites. However, in 1996, the annual mean (± s.e.) abundance was significantly higher (ANOVA; $p < 0.001$) in eels from site 3 (0.26 ± 0.07 parasites/eel) than in eels from all other sites except pots (Figure 26a). The annual prevalence of *B. claviceps* was highest at sites 1-3 (~ 6-13%). Among infested eels, there was no significant difference in annual mean intensity in eels from the various sample sites. No significant relationship existed among size of eel and annual prevalence, mean abundance or mean intensity of *B. claviceps* (Figure 26a). From month to month, there were no significant differences in annual prevalence (Appendix B1), mean abundance or mean intensity of *B. claviceps*. Immature specimens and gravid forms were equally

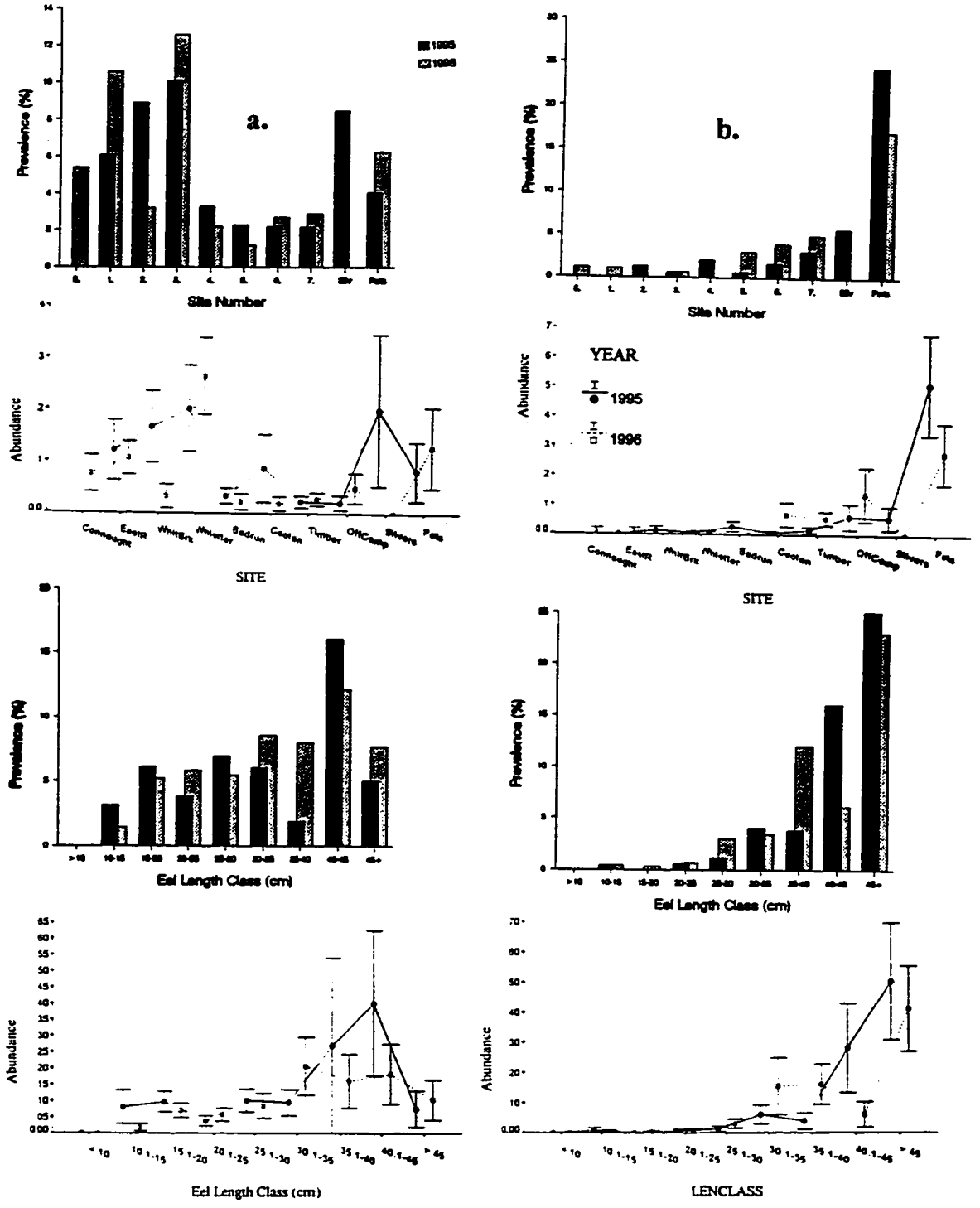


Figure 26. Annual prevalence (%) and mean (± s.e.) abundance of : (a.) *Bothriocephalus claviceps* and (b.) *Proteocephalus macrocephalus* at each sample site and for each eel length class during 1995 and 1996.

common from month to month.

Despite the rarity of the second cestode, *Proteocephalus macrocephalus*, the annual prevalence (%) and mean (± s.e.) abundance was highest (G-test, $p < 0.05$; ANOVA; $p < 0.001$ respectively) among potted eels (24.5%, 0.51 ± 0.17 parasites/eel in 1995; 17.0%, 0.28 ± 0.10 parasites/eel in 1996; Figure 26b). Among infested eels, there was no significant difference in annual mean intensity of *P. macrocephalus* from site to site. Eels greater than 45 cm had the highest (G-test, $p < 0.05$; ANOVA; $p < 0.001$) annual prevalence and mean abundance, respectively (25.0%, 0.50 ± 0.19 parasites/eel in 1995; 23.0%, 0.41 ± 0.14 parasites/eel in 1996; Figure 26b). There were no significant differences in annual mean intensity of *P. macrocephalus* among the various length classes of infested eels. From month to month, there was no significant differences in annual prevalence, mean abundance or mean intensity of *P. macrocephalus*. About 75% of all specimens found were immature.

The acanthocephalan, *Pomphorhynchus bulbocolli*, was absent from site 1 and only one specimen was found from one eel at site 8. It was also rare at site 4 and among all silver eels collected. Annual prevalence and mean abundance was highest in potted eels (18.5%, 0.52 ± 0.19 parasites/eel in 1995; 12.7%, 0.34 ± 0.15 parasites/eel in 1996), but was similar at the remaining sites (Figure 27a). Among infested eels, annual mean intensity of *P. bulbocolli* was not significantly different from site to site. The highest mean annual abundance of *P. bulbocolli* was in eels greater than 45 cm (0.55 ± 0.35 parasites/eel in 1995; 0.51 ± 0.27 parasites/eel in 1996). Eels up to 45 cm had similar annual mean abundances (~ 0.07-0.17 parasites per eel). The annual prevalence of *P. bulbocolli* was

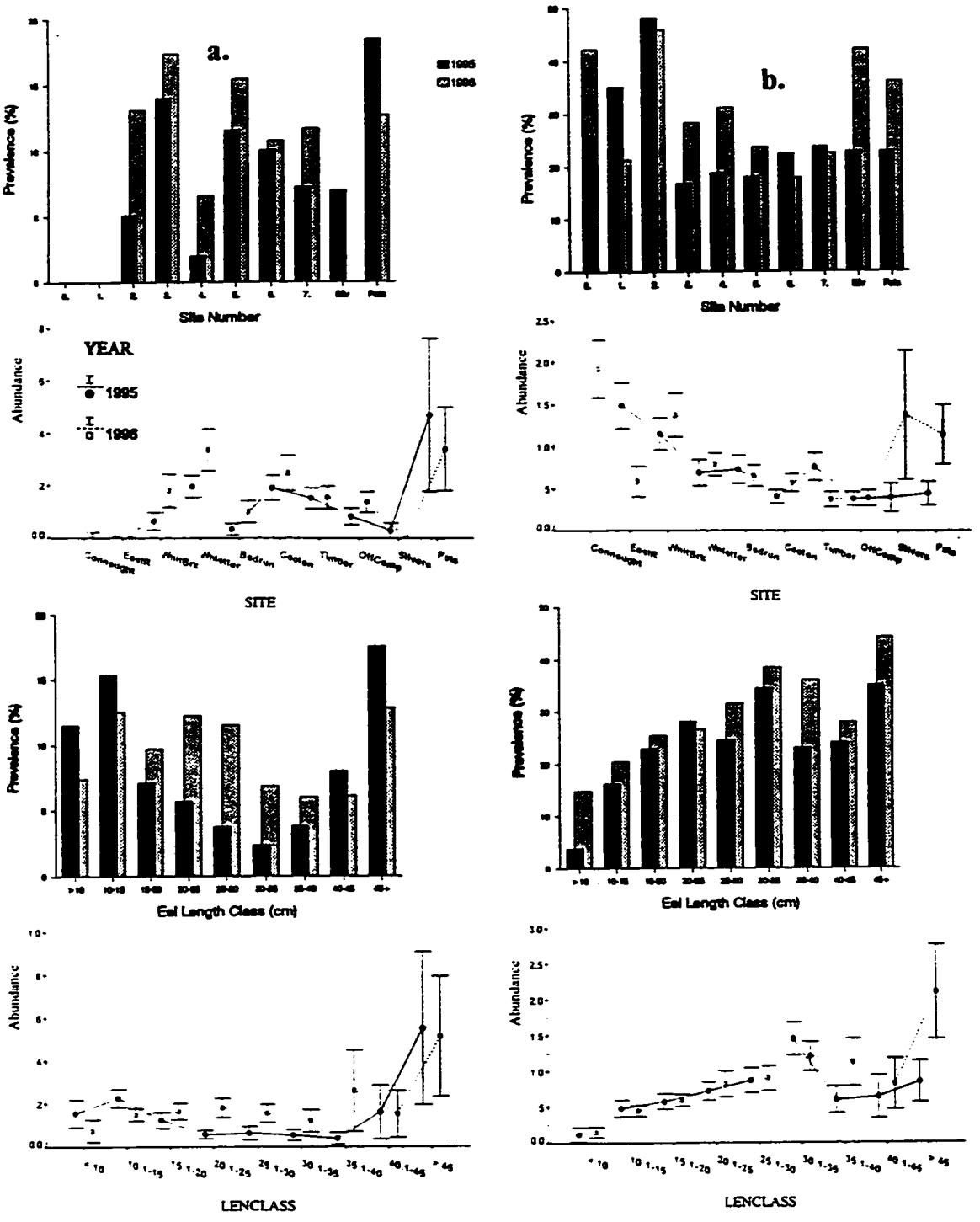


Figure 27. Annual prevalence (%) and mean (± s.e.) abundance of : (a.) *Pomphorhynchus bulbocolli* and (b.) *Paraquimperia tenerrima* at each sample site and for each eel length class during 1995 and 1996.

bimodal with peaks at each length extreme (> 45 cm : ~ 12.8-17.5%; < 15 cm: ~ 12.5-15%; Figure 27a). There was no significant difference in mean intensity among the size classes of infested eels. On a monthly comparison, the highest annual prevalence (Appendix B1) and mean abundance of *P. bulbocolli* was in October (29.2%, 0.41 ± 0.07 parasites/eel in 1995; 22.3%, 0.28 ± 0.06 parasites/eel in 1996), but no monthly differences were observed in mean intensity among infested eels. More than 90% of all specimens did not attain full maturity; gravid females were rare (< 5%).

The ubiquitous nematode, *Paraquimperia tenerrima*, was most abundant at the sites of lowest pH (sites 8, 1-2). In 1995, the annual prevalence (%) and mean (± s.e.) abundance was highest (G-test, $p < 0.05$; ANOVA; $p < 0.001$ respectively) at site 1 (35.1%, 1.50 ± 0.27 parasites/eel) and site 2 (48.1%, 1.13 ± 0.18 parasites/eel; Figure 27b). Among infested eels, site 1 also had the highest (ANOVA, $p < 0.001$) annual mean intensity (4.27 ± 0.56 parasites/infested eel). In 1996, the annual prevalence (%) and mean abundance was highest (G-test, $p < 0.05$; ANOVA; $p < 0.001$) at sites 8 & 2 and in large silver and potted eels (~ 36-45%, ~ 1.1 - 1.9 parasites/eel; Figure 27b). Among infested eels, annual mean intensity was significantly highest at site 8 (4.54 ± 0.60 parasites/infested eel). Among the different length classes of eels, the highest (G-test, $p < 0.05$; ANOVA; $p < 0.001$) annual prevalences (%) and mean (± s.e) abundances (respectively) were in eels 30-35 cm (34.4%, 1.45 ± 0.23 parasites/eel in 1995; 38.4%, 1.20 ± 0.20 parasites/eel in 1996) and 45+ cm (35.0%, 0.85 ± 0.65 parasites/eel in 1995; 44.0%, 2.10 ± 0.65 parasites/eel in 1996; Figure 27b). There was no significant difference in mean intensity of *P. tenerrima* during 1995 among eel length classes, but in 1996, the

mean intensity in eels 45+ cm (4.82 ± 1.23 parasites/infested eel) was highest (ANOVA; $p < 0.05$). From month to month, the highest (G-test, $p < 0.05$; ANOVA; $p < 0.001$) annual prevalence (Appendix B1) and mean abundance (respectively) of *P. tenerrima* was during June (45.0%, 1.34 ± 0.15 parasites/eel in 1995; 47.8%, 1.44 ± 0.15 parasites/eel in 1996). Peaks in prevalence and abundance in June coincided with 90% of all specimens being sexually mature or gravid. From July to October, and the following May, most individuals were sexually immature.

The gill copepod, *Ergasilus celestis*, was absent from site 8, but was common at all remaining sites. The highest (G-test, $p < 0.05$; ANOVA; $p < 0.001$) annual prevalence (%) and mean (± s.e.) abundance (respectively) was in potted eels (92.0%, 15.04 ± 2.62 parasites/eel in 1995; 97.8%, 15.61 ± 2.68 parasites/eel in 1996; Figure 28a). Among electrofished eels, the highest (G-test, $p < 0.05$; ANOVA; $p < 0.01$) annual prevalences (%) and mean (± s.e.) abundances (respectively) were in silver eels (37.1%, 2.31 ± 0.64 parasites/eel in 1995; 46.1%, 3.38 ± 1.13 parasites/eel in 1996; Figure 28a) and eels from site 7 (40.0%, 2.34 ± 0.47 parasites/eel in 1995; Figure 28a). Among infested eels, annual mean intensity was highest (ANOVA; $p < 0.001$) in potted eels (16.37 ± 2.77 parasites/ infested eel in 1995; 15.95 ± 2.72 parasites/infested eel in 1996). The abundance of *E. celestis* was postively correlated with pH and negatively correlated with flow rate ($r = 0.289$, $p < 0.05$; $r = -0.414$, $p < 0.001$ respectively). As length of eel increased, there was a progressive increase in annual prevalence and mean abundance of *E. celestis*, such that values of each eel length class were significantly larger (ANOVA; $p < 0.001$) than the previous (Figure 28a). Among infested eels, annual mean intensity was highest (ANOVA;

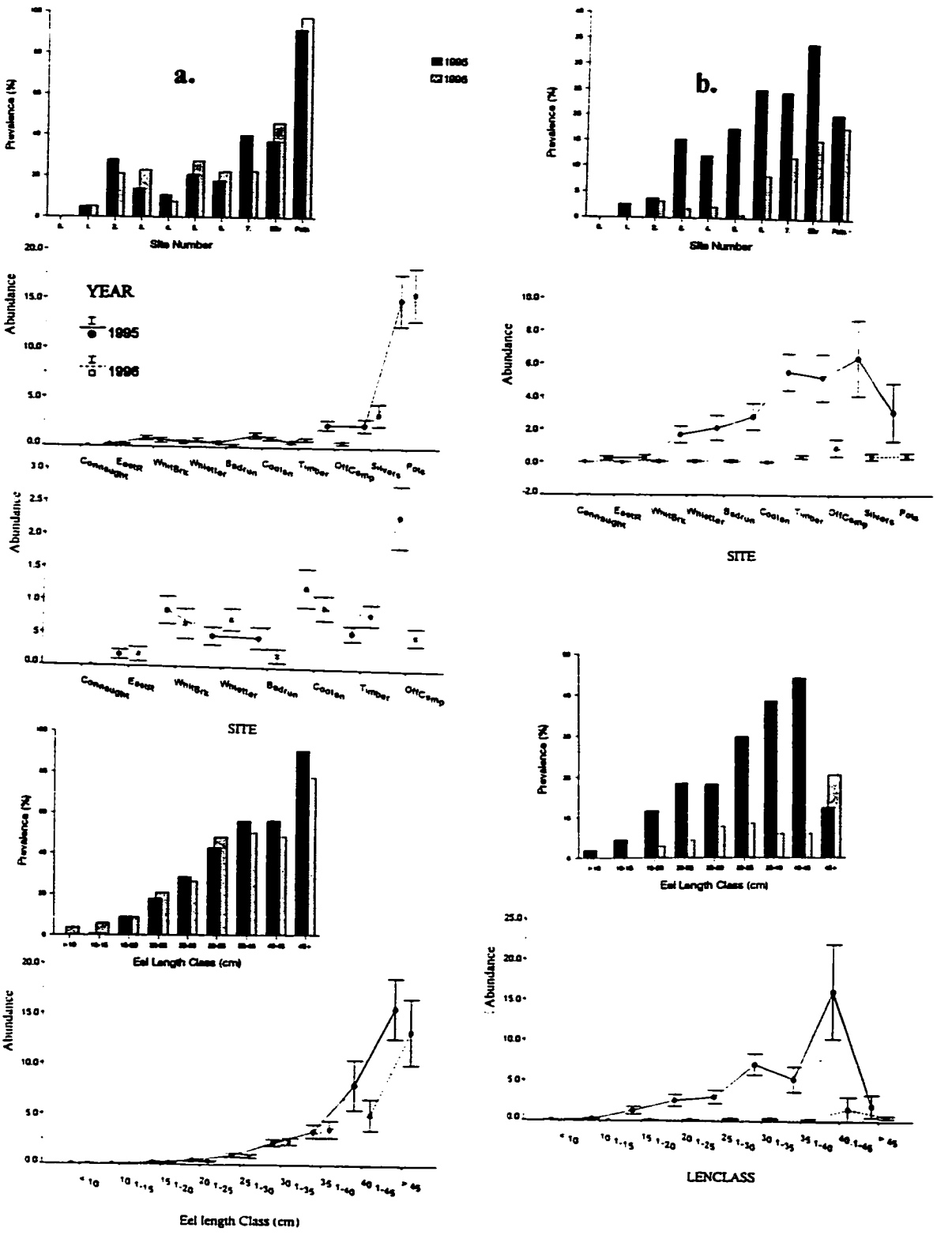


Figure 28. Annual prevalence (%) and mean (± s.e.) abundance of : (a.) *Ergasilus celestis* and (b.) *Pseudodactylogyrus anguillae* at each sample site and for each eel length class during 1995 and 1996.

$p < 0.001$) in eels greater than 40 cm (~ 8.0-17.3 parasites/infested eel). In 1995, there were no significant differences in total mean abundance nor intensity per month, but in 1996, mean (± s.e) abundance was highest (ANOVA; $p < 0.01$) in July (2.60 ± 0.51 parasites/eel). Similarly, monthly peaks in prevalence occurred in July (~ 22-32%) and August (~ 22-31%; Appendix B1). Embryo ('egg') cases could be found from specimens during any month, but in July and August over 95% of all specimens had 'maturing' embryo cases. During October and May, less than 10% of specimens had embryo cases.

The gill monogene, *Pseudodactylogyrus anguillae*, was absent from site 8 and was rare at sites 1 (only present in 1995) and 2. In 1995, the annual prevalence (%) and mean (± s.e.) abundance was highest (G-test, $p < 0.05$; ANOVA; $p < 0.01$ respectively) in silver eels (34.2%, 6.37 ± 2.29 parasites/eel) and in eels from sites 6 (25.2%, 5.51 ± 1.11 parasites/eel) and 7 (24.7%, 5.17 ± 1.42 parasites/eel; Figure 28b). In 1996, the annual prevalence (%) and mean (± s.e.) abundance was highest at site 7 (11.9%, 0.90 ± 0.51 parasites/eel). Among infested eels, there were no significant differences in annual mean intensity from site to site during 1995 and 1996. The abundance of *P. anguillae* was postively correlated with pH and negatively correlated with flow rate ($r = 0.473$, $p < 0.001$; $r = -0.600$, $p < 0.001$ respectively). There was a gradual increase in annual prevalence and mean abundance of *P. anguillae* as the length of eels increased to 40-45 cm, where these values peaked (44%, 16.12 ± 5.89 parasites/eel in 1995; G-test, $p < 0.05$; ANOVA; $p < 0.001$ respectively; Figure 28b). Eels larger than 45 cm had low annual prevalences and mean abundances (< 12%, 1.90 ± 1.38 parasites/eel). In 1995, July and August had the highest (G-test, $p < 0.05$; ANOVA; $p < 0.001$) annual prevalences

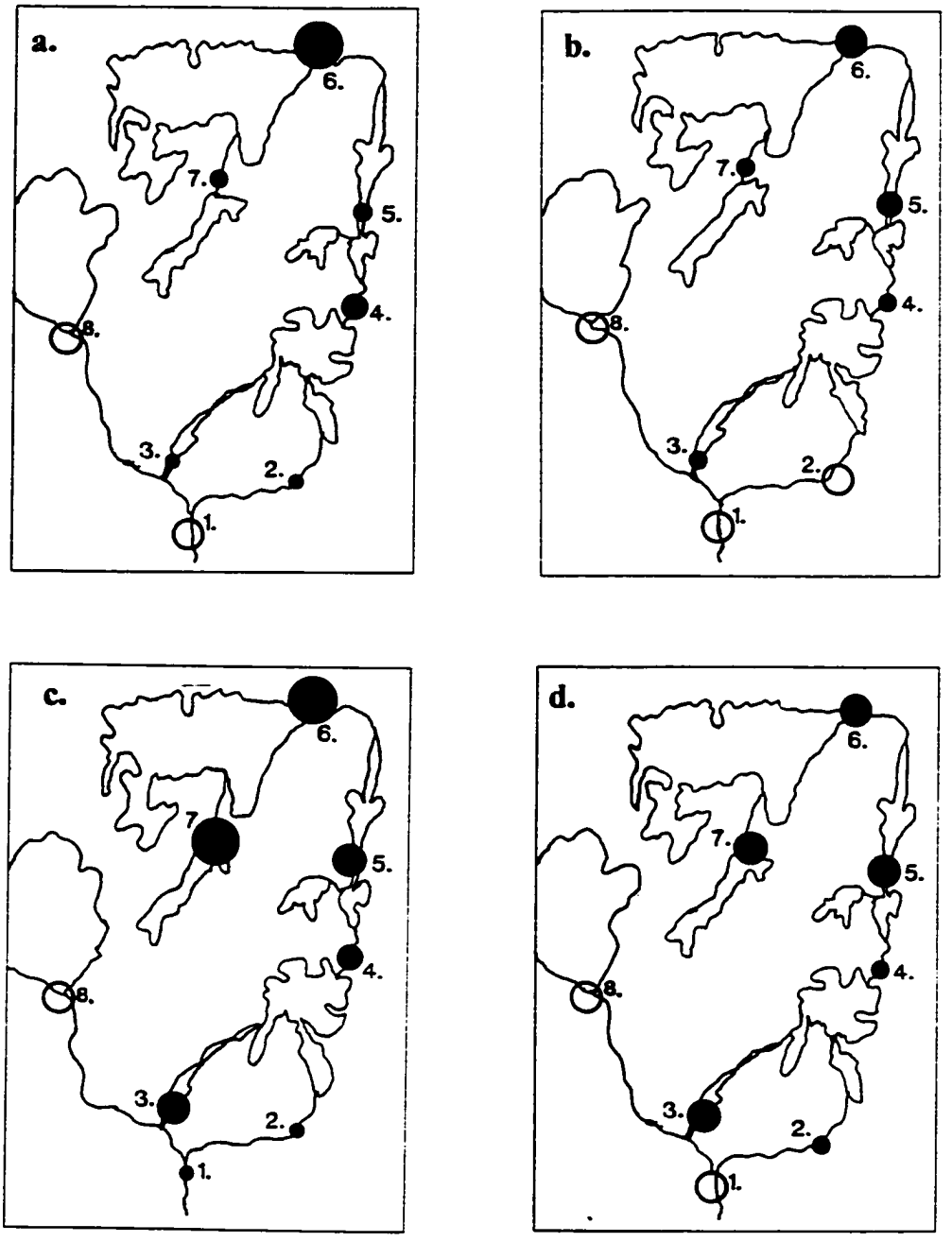


Figure 29a. Spatial dynamics of : (a.) *Crepidostomum brevivitellum* (b.) *Azygia longa* (c.) *Pseudodactylogyrus anguillae* and (d.) *Pomphorhynchus bulbocolli* in the Timber lake watershed.

(Prevalences: ○ Absent ● < 5% ● 5-10% ● 10-15% ● 15-20% ● > 20%)

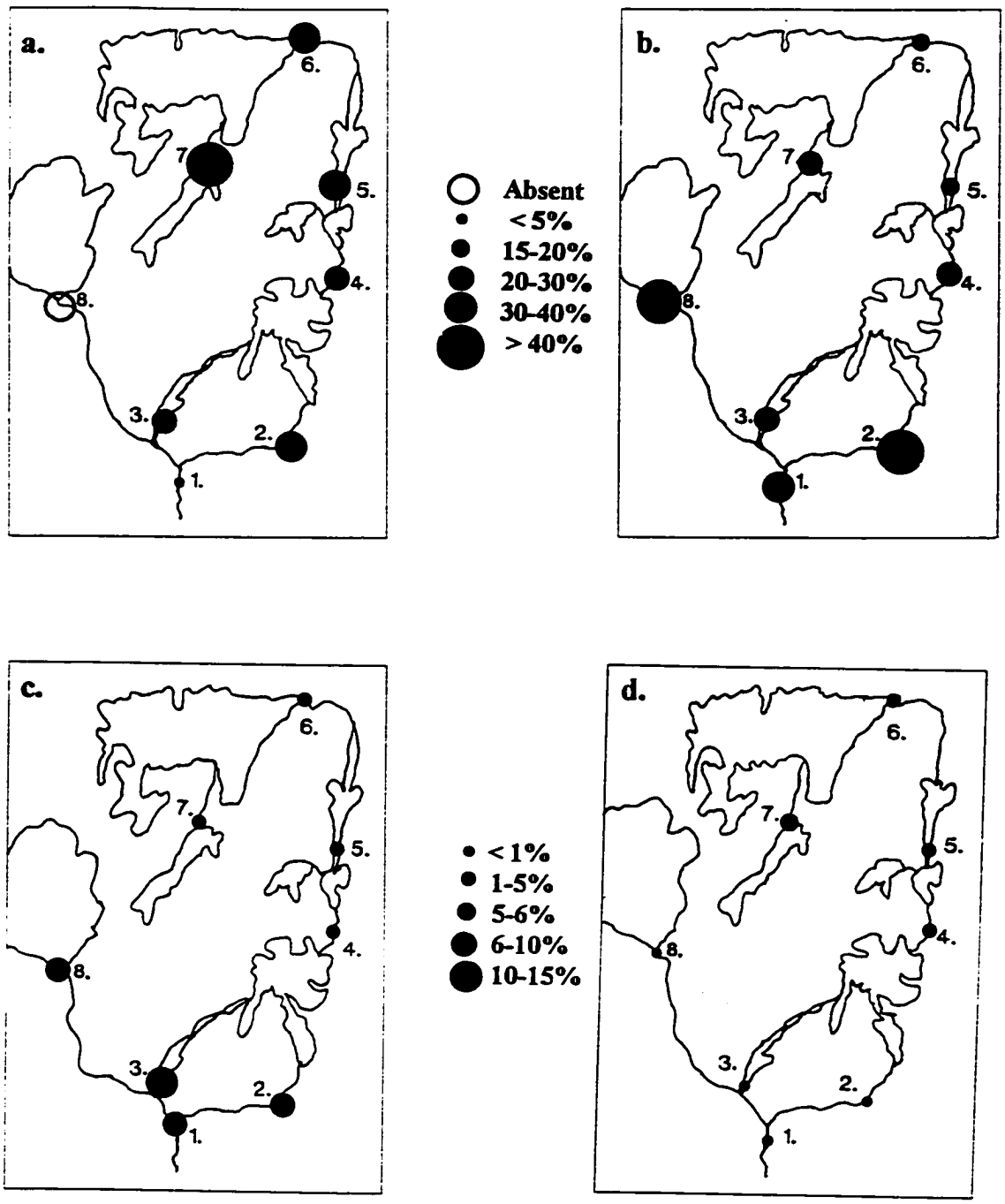


Figure 29b. Spatial dynamics of : (a.) *Ergasilus celestis* (b.) *Paraquimperia tenerrima*(c.) *Bothriocephalus claviceps* and (d.) *Proteocephalus macrocephalus* in the Timber lake watershed.

(Appendix B1) and mean abundances respectively (~ 25-27%, ~ 5.00 parasites/eel). There were no significant differences in annual prevalence, mean abundance and mean intensity from month to month in 1996.

Overall, the parasites of electrofished eels were most abundant at various points along the watershed, displaying a 'patchy' distribution. Both species of digenes, the gill monogene, the acanthocephalan and the gill copepod were concentrated at the upper reaches of the watershed, at sites of low flow and high pH (Figure 29a; b). The nematode, *P. tenerrima*, and the cestode, *B. claviceps*, were most abundant at the lower reaches and most acidic sites of the watershed (Figure 29b). The cestode, *P. macrocephalus*, was ubiquitous but rare, being slightly more abundant in the upper reaches of the watershed (Figure 29b).

With the exception of the monogene, *P. anguillae*, there was a pattern of consistency in the actual total numbers (sums) of each parasite species from each sample site from 1995 to 1996 (Appendix B2).

Community Composition Dynamics

Only 5 species of intestinal helminths (of a possible 9) dominated (numerically) the component community. The specialist, *P. tenerrima*, dominated most component communities (71.6%), followed by the specialist *C. brevivitellum* (10.8%), and generalist *P. bulbocolli* (10.8%), then the generalist *A. longa* (5.4%) and finally, the specialist *B. claviceps* (1.4%).

Monthly variation was common among the helminth component communities such

8. Connaught Lake

Parasite Species	Month 1996					
	May	June	July	August	Sept.	Oct
C. brevivitellum	-	-	-	-	*	*
A. longa	-	-	-	-	*	*
B. claviceps	-	03	06	-	*	*
P. macrocephalus	05	-	-	-	*	*
P. bulbocolli	-	01	-	-	*	*
P. tenerrima	.95	.96	.94	1.0	*	*
Helminth Richness	2	3	2	1	*	*

1. East River

Parasite Species	Month 1995 (1996)					
	May	June	July	August	Sept.	Oct
C. brevivitellum	- (-)	- (-)	- (-)	- (*)	- (-)	* (*)
A. longa	- (-)	- (-)	- (-)	- (*)	- (-)	* (*)
B. claviceps	07 (13)	05 (.09)	08 (.33)	11 (*)	12 (.19)	* (*)
P. macrocephalus	- (13)	- (-)	- (-)	- (*)	- (-)	* (*)
P. bulbocolli	- (-)	- (-)	- (-)	- (*)	- (-)	* (*)
P. tenerrima	**.93 (.75)**	**.95 (.91)**	**.92 (.67)**	**.89** (*)	**.88 (.81)**	* (*)
Helminth Richness	2 (3)	2 (2)	2 (2)	2 (*)	2 (2)	* (*)

2. Whitford Brook

Parasite Species	Month 1995 (1996)					
	May	June	July	August	Sept.	Oct
C. brevivitellum	- (17)	- (-)	- (05)	**.80** (*)	* (*)	* (*)
A. longa	- (-)	- (-)	- (-)	- (*)	* (*)	* (*)
B. claviceps	21 (-)	07 (02)	10 (05)	- (*)	* (*)	* (*)
P. macrocephalus	- (-)	- (-)	- (-)	- (*)	* (*)	* (*)
P. bulbocolli	- (17)	09 (04)	- (19)	20 (*)	*(*)	* (*)
P. tenerrima	**.79 (.66)**	**.84 (.94)**	**.91 (.71)**	- (*)	* (*)	* (*)
Helminth Richness	2 (3)	3 (3)	2 (4)	2 (*)	* (*)	*(*)

Table 4a. Monthly component community composition for sites: 8, 1 and 2. (Values in table expressed as proportion of total numeric sum of all helminths. Values in bold type represent numerically dominant species.) (* = no sample taken, - = species absent from sample)

3. Whistler Lake

Parasite Species	Month 1995 (1996)					
	May	June	July	August	Sept.	Oct
C. brevivitellum	- (05)	- (.03)	- (.04)	08 (-)	- (.06)	03 (.10)
A. longa	07 (02)	- (.07)	05 (.17)	04 (.04)	- (.13)	25 (.15)
B. claviceps	.13(.14)	03 (.12)	20 (.12)	**.63** (.32)	.11(.25)	22 (.30)
P. macrocephalus	- (02)	- (-)	- (-)	04 (-)	- (-)	- (-)
P. bulbocolli	3 (-)	04 (.14)	05 (.25)	16 (.46)	**37 (.31)**	**.41 (.35)**
P. tenerrima	**.77 (.76)**	**.92 (.64)**	**.70 (.42)**	04 (.18)	**.51** (.25)	09 (10)
Helminth Richness	4 (5)	3 (5)	4 (5)	6 (4)	3 (5)	5(5)

4. Bad Lake Run

Parasite Species	Month 1995 (1996)					
	May	June	July	August	Sept.	Oct
C. brevivitellum	13 (.27)	02 (.19)	**47 (.38)**	28 (*)	19 (*)	* (*)
A. longa	- (-)	02 (.02)	- (.08)	**.50** (*)	06 (*)	* (*)
B. claviceps	- (-)	07 (.04)	- (-)	- (*)	13 (*)	* (*)
P. macrocephalus	03 (-)	- (-)	- (-)	06 (*)	- (*)	* (*)
P. bulbocolli	- (19)	02 (04)	- (08)	09 (*)	06 (*)	* (*)
P. tenerrima	**.84 (.54)**	**.85 (.70)**	**.53 (.46)**	06 (*)	**.56** (*)	* (*)
Helminth Richness	3 (3)	5 (5)	2 (4)	5 (*)	5 (*)	*(*)

5. Coolan Lake

Parasite Species	Month 1995 (1996)					
	May	June	July	August	Sept.	Oct
C. brevivitellum	13 (.21)	03 (.05)	- (28)	04 (.09)	17 (10)	25 (.26)
A. longa	12 (03)	03 (03)	34 (22)	**.39** (09)	08 (05)	07 (09)
B. claviceps	13 (-)	34 (-)	- (03)	- (-)	- (-)	04 (06)
P. macrocephalus	- (11)	- (08)	- (-)	- (-)	- (-)	02 (03)
P. bulbocolli	- (11)	- (.05)	06 (.06)	**.39** (36)	**.67 (.80)**	25 (26)
P. tenerrima	**.52 (.60)**	**.60 (.79)**	**.59 (.41)**	17 (.45)	08 (05)	**.36 (.31)**
Helminth Richness	4 (5)	4 (5)	3 (5)	4 (4)	2 (2)	6 (6)

Table 4b. Monthly component community composition for sites: 3-5. (Values in table expressed as proportion of total numeric sum of all helminths. Values in bold type represent numerically dominant species.) (* = no sample taken, - = species absent from sample)

6. Timber Lake

Parasite Species	Month 1995 (1996)					
	May	June	July	August	Sept.	Oct
C. brevivitellum	26 (.09)	24 (.55)	26 (.64)	.69 (.44)	.61 (.53)	38 (.26)
A. longa	21 (.06)	17 (.02)	- (.14)	05 (.17)	17 (.18)	03 (.46)
B. claviceps	- (-)	04 (.02)	- (.03)	- (.01)	01 (.03)	- (.03)
P. macrocephalus	05 (.03)	01 (-)	- (-)	01 (-)	- (-)	- (.06)
P. bulbocolli	05 (.06)	06 (.02)	14 (.06)	04 (.19)	19 (.11)	08 (.17)
P. tenerrima	.42 (.77)	.47(.38)	.59 (.14)	20 (.19)	08 (.06)	.50 (.03)
Helminth Richness	5 (5)	6 (5)	3 (5)	5 (5)	5 (5)	4 (6)

7. Officer's Camp Lake

Parasite Species	Month 1995 (1996)					
	May	June	July	August	Sept.	Oct
C. brevivitellum	- (.06)	- (.22)	- (.44)	.33 (.13)	* (*)	* (*)
A. longa	- (.06)	.21 (.02)	.08 (.06)	.08 (.60)	* (*)	* (*)
B. claviceps	- (-)	.03 (.08)	- (-)	.08 (-)	* (*)	* (*)
P. macrocephalus	38 (-)	- (.23)	08 (-)	- (-)	* (*)	* (*)
P. bulbocolli	- (.35)	- (.05)	25 (.06)	.42 (.27)	* (*)	* (*)
P. tenerrima	.61 (.53)	.75 (.40)	.58 (.44)	08 (-)	* (*)	* (*)
Helminth Richness	2 (4)	3 (6)	4 (4)	5 (3)	* (*)	*(*)

Table 4c. Monthly component community composition for sites: 6 and 7. (Values in table expressed as proportion of total numeric sum of all helminths. Values in bold type represent numerically dominant species.) (* = no sample taken, - = species absent from sample)

that one species was not the only numerically dominant member of the community for every month. Such a pattern only applied to the 'species -poor' component communities at sites 8 and 1, where the specialist, *P. tenerrima*, was the dominant intestinal helminth during every month of 1995 and 1996 (Table 4a). Excluding site 6, *P. tenerrima* was the dominant helminth at all sites from May to July, after which either species of digene or the acanthocephalan would dominate the component communities at the sites of highest pH (4-7; Tables 4b; c). In addition, the proportion of dominance of *P. tenerrima* at sites 5-7 was seldom above 0.50, while at the remaining sites it was seldom below 0.70. At site 6, most helminths were found in similar numerical proportions from month to month - a condition rarely observed among the other component communities.

Ecological Indices

During 1995 and 1996, the mean intestinal helminth component community species richness was highest (ANOVA; $p < 0.001$) at sites 3-7 (~ 3.8-5.0 helminth spp/site) and lowest at sites 8, 1-2 (~ 2.0-2.85 helminth spp/site; Figure 30a). Similarly, mean indices of diversity were highest (ANOVA; $p < 0.001$) at sites 3-7 (Shannon Index: ~ 0.93-1.13; Hill's N2: ~ 2.3-2.8) and lowest at sites 8, 1-2 (Shannon Index: ~ 0.15-0.56; Hill's N2: ~ 1.1-1.7; Figure 30b; c). Conversely, mean dominance index (Simpson) was lowest at sites 3-7 (~ 0.38-0.53) and highest at sites 8, 1-2 (~ 0.64-0.93; Figure 30d). Mean values of Pielou's Index of evenness per sample site had the same patterns as the diversity indices (highest at sites 3-7; ~ 0.69-0.84).

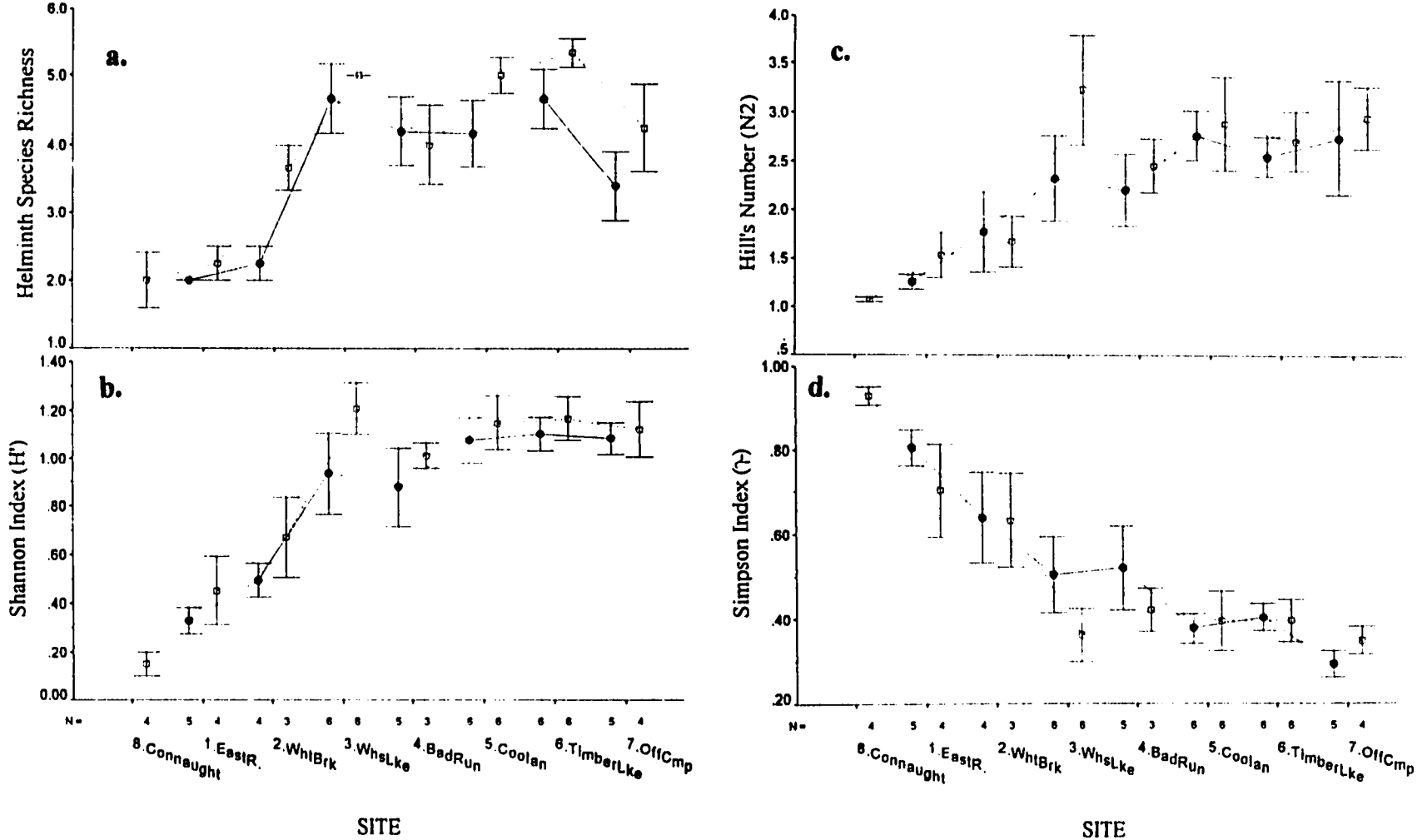


Figure 30. Annual mean (± s.e.): (a.) species richness; (b.) Shannon Index of Diversity (H'); (c.) Hill's Index of Diversity (N2) and (d.) Simpson Index of Dominance (λ) of the intestinal helminth component communities during 1995 and 1996.

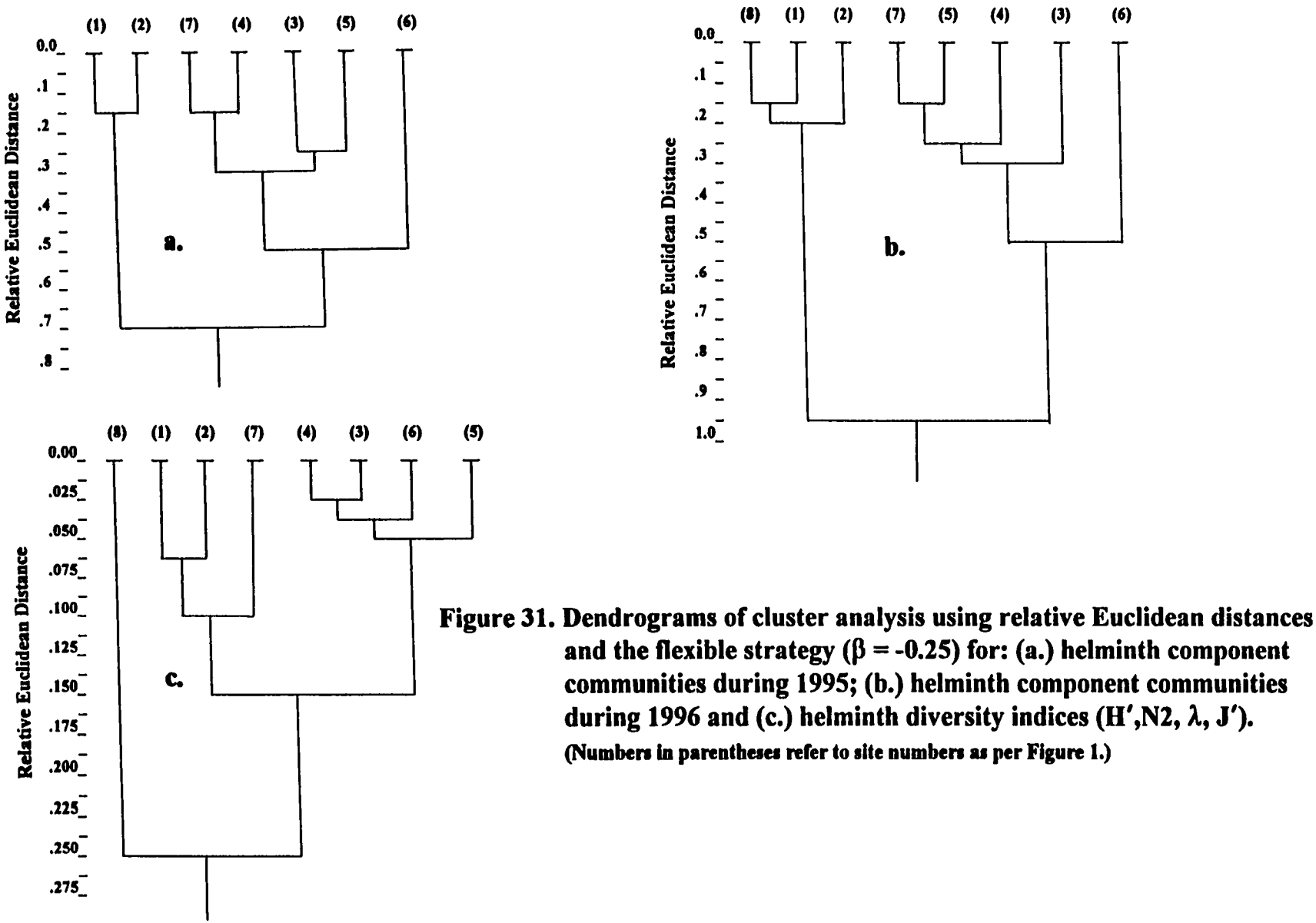


Figure 31. Dendrograms of cluster analysis using relative Euclidean distances and the flexible strategy ($\beta = -0.25$) for: (a.) helminth component communities during 1995; (b.) helminth component communities during 1996 and (c.) helminth diversity indices (H′,N2, λ, J′).
(Numbers in parentheses refer to site numbers as per Figure 1.)

Community Classification and Ordination

A cluster analysis (using realtive Euclidean distances and a flexible strategy with β = -0.25) of the helminth abundances among component communities during 1995 was similar to that constructed for the 1996 data (Figure 31a; b). In both dendrograms, the two main cluster groups defined are: (i) sites 3-7 and (ii) sites1, 2 and 8 (in 1996). A second cluster analysis (using realtive Euclidean distances and a flexible strategy with β = -0.25) on the helminth community diversity indices (1995 and 1996 pooled) produced a comparable dendrogram to that based on helminth abundance (Figure 31c) . The only difference was that site 7 was now 'clustered' within group (ii) - sites 1, 2 and 8.

Results of correspondence ordination on the same component community data (Figure 32), produced similar patterns (for 1995 and 1996) to the cluster classification. Components 1 and 2 accounted for 87.3 % and 86.1% of the variation among ordination scores of component communities in 1995 and 1996 respectively. The ordination of sites 1, 2 and 8 were determined by the abundance of the nematode, *P. tenerrima*, while the ordination of sites 4 and 6 were determined by the abundance of the digene, *C. brevivitellum* (Figure 32). Site 3 was positioned on the abundance of the cestode, *B. claviceps*, while the remaining sites (5 and 7) were positioned on a combination of the abundances of the digene, *A. longa* and the acanthocephalan, *P. bulbocolli* (Figure 32). The rare cestode, *P. macrocephalus*, contributed little to site ordination in 1995, but was more important (and more abundant) to the ordination of sites 5-7 in 1996.

Multiple linear regression analysis of the ordination axis on the environmental variables pH, flow rate and distance from sea resulted in pH being the only factor

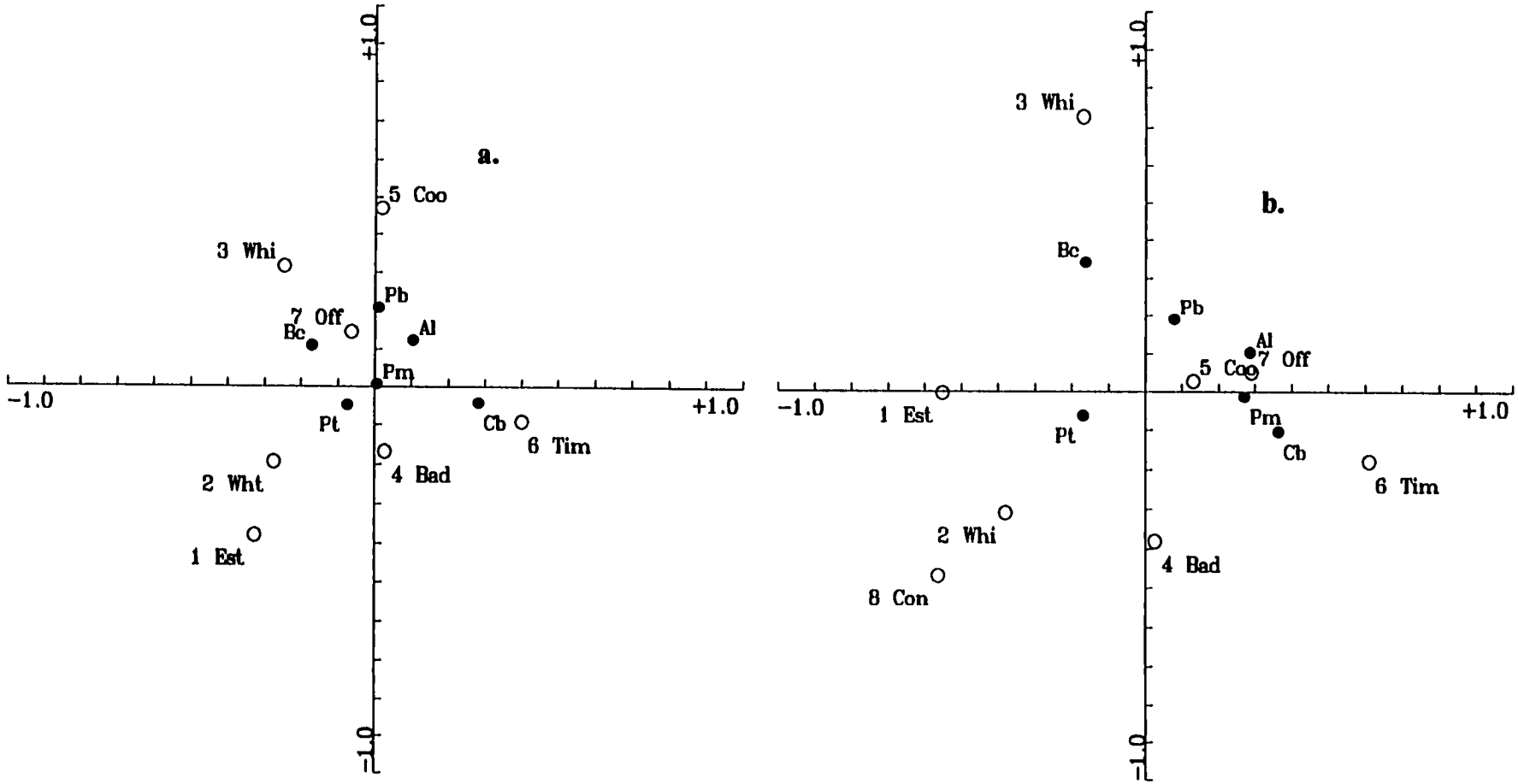


Figure 32. Ordination results of correspondence analysis using species abundances of the helminth component communities during: (a.) 1995 and (b.) 1996.

(C.b. = *Crepidostomum brevivitellum*, A.l. = *Azygia longa*, B.c. = *Bothriocephalus claviceps*, P.m. = *Proteocephalus macrocephalus*, P.b. = *Pomphorhynchus bulbocolli*, P.t. = *Paraquimperia tenerrima*

significantly ($r^2 = 0.853, p < 0.025$ in 1995; $r^2 = 0.875, p < 0.01$ in 1996) related to the ordination scores of each sample site along axis 1. The percent contibution of pH in explaining the variation in sample site ordination scores along axis 1 was 98.4 % in 1995 and 90.9% in 1996. No other significant relationships existed among the remaining environmental variables and ordination scores of the sample sites.

Richness Patterns between Infra- and Component Communities

As helminth richness of the component community increased, infracommunity richness did not increase in a linear 1:1 ratio. Maximum helminth infracommunity richness seldom exceeded 3 species, when component community richness was as high as 6 (Figure 33a). The same pattern existed when gill parasites were included. The richness of the parasite assemblage at any site could be as high as 9-11, but the maximum parasite assemblage per eel would not exceed 6, and was often 5 or less (Figure 33b).

Applicability as 'Bio-tags'

When silver eels were included with data from yellow eels, monthly 'peaks' in eel length at site 5 downstream to site 1 corresponded to 'peaks' in abundance of the parasites *A. longa* and *E. celestis* during 1995 and 1996 (Figure 34). These peaks begin at site 5 in July and progress to August and September at downstream sites, then disappear by October. Yellow eels from sites 1 and 2 were never parasitized by the digene *A. longa*, it was only recovered from silver eels at these sites. Silver eels were absent from site 2 in 1995, but were present in 1996, corresponding to an appearance of the digene, *A.* longa. In addition, the silver eels at sites 1 and 2 had higher abundances of *E. celestis* on their

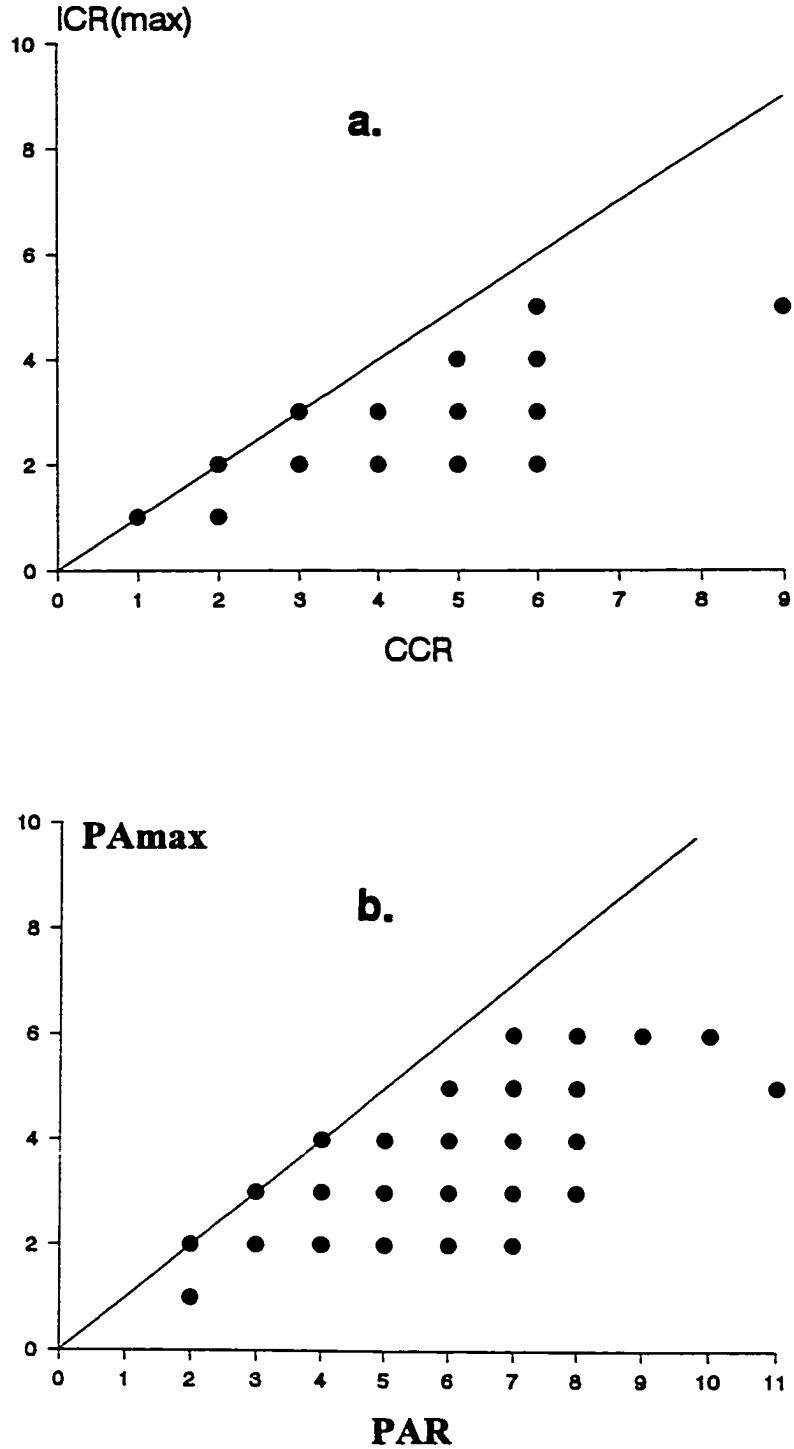


Figure 33. Scatterplots of: (a.) helminth component community richness (CCR) and maximum helminth infracommunity richness (ICRmax) and (b.) parasite assemblage richness per site (PAR) and maximum parasite assemblage richness per eel (PAmax).

(Solid line in figure represents hypothetical 1:1 linear relationship between CCR and ICR.)

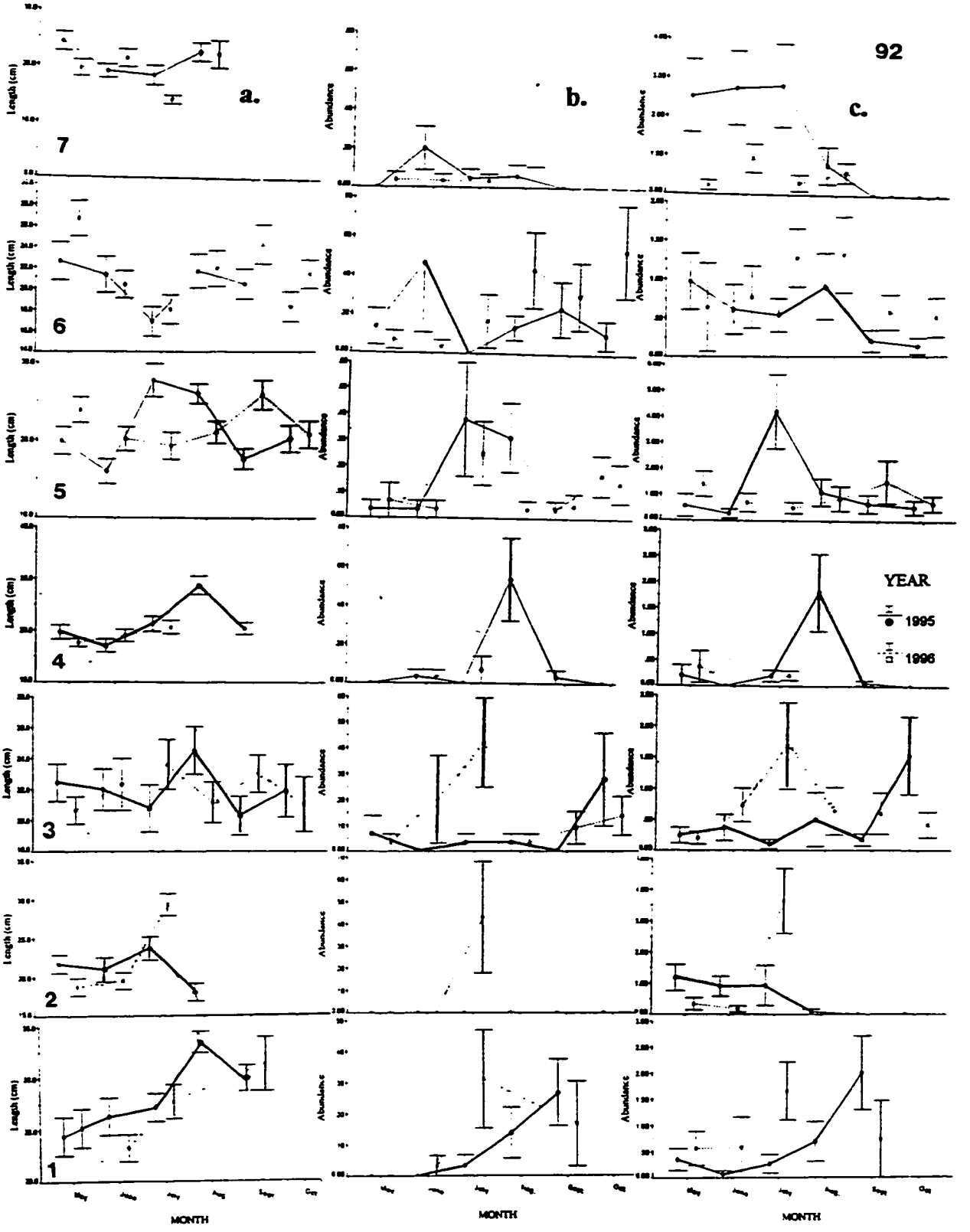


Figure 34. Monthly mean (± s.e.) : (a.) eel length; (b.) abundance of *Azygia longa* and (c.) abundance of *Ergasilus celestis.*

(Numbers in graphs refer to site numbers as per Figure 1.)

gills than did yellow eels (of the same size range) at these sites. These concomittant peaks in mean eel length and abundances were absent from sites 6-8.

When silver eels were added to the previously described cluster analyses and treated as an additional 'sample site', they clustered with site pair 3 and 5 in 1995 and with site 3 in 1996.

3.5 Benthic Stream Macroinvertebrate Assemblages

The highest maximum richness (number of invertebrate families) was at site 6 (38 families), while the lowest was at site 8 (16 families), site 2 (19 families) and site 1 (20 families). The remaining sites had similar values of maximum richness (~23-27 families; Table 5). Chironomidae (midge larvae) was the numerically dominant invertebrate family at sites 1, 2, 7 and 8; while Sphaeridae (clams) was the dominant taxon at sites 4 - 6 (Table 5). The amphipods (Gammaridae) were the most dominant taxon at site 3. Overall, the caddisfly larvae (Tichoptera) comprised the most abundant invertebrate order having the greatest diversity of families (max. 7 at sites 4 - 6). The high richness at sites 4-7 was the result of the addition of more families of aquatic insects (Gomphidae and Agrionidae of the Odonata; Heptageniidae of the Ephemeroptera; Leuctridae of the Plecoptera; Helicopsychidae and Hydroptilidae of the Trichoptera; Psephenidae of the Coleoptera; Rhagionidae, Tabanidae and Tipulidae of the Diptera) as well as many non-arthropod species: molluscs (bivalves and gastropods); annelids (oligochaetes and hirudineans); nematodes and turbellarians. (Refer to Appendix C for a complete listing of taxa and total abundance per sample site.)

Variable	Site Number 1.	2.	3.	4.	5.	6.	7.	8.
Maximum Richness (No. Families)	20	19	23	28	25	38	27	16
Dominant Family (%)	Chiron. 45.8%	Hydropsych. 26.2%	Gammar. 22.1%	Sphaeridae 15.7%	Sphaeridae 29.6%	Sphaeridae 13.8%	Chiron. 26.9%	Chiron. 40%
Dominant Order (%)	Diptera 47.0%	Trichoptera 36.7%	Trichoptera 23.6%	Tricho. 34.0%	Bivalvia 29.6%	Trichoptera 17.8%	Tricho. 31.6%	Tricho. 59.8%
Biomass (No. individuals/m²)	57	295	196	284	247	216	186	133

Table 5. Maximum richness, dominant taxa and biomass (number of individuals/m²) of the benthic stream macroinvertebrate assemblages at each sample site during August 1996.
(Chiron. = Chironomidae; Hydropsych. = Hydropsychidae; Gammar .= Gammaridae; Dominance values expressed as the numerical percentage of individuals)

The greatest biomass (density) was at sites 2 and 4 (295 and 284 invertebrates/m^2 respectively) and the lowest was at site 1 (57 invertebrates/m^2) and site 8 (133 invertebrates /m^2; Table 5).

Ecological Indices

Trends in ecological indices for the invertebrate assemblages among the various sample sites were comparable to the trends observed among the helminth component community data. The mean richness was highest (ANOVA; $p < 0.01$) at sites 3-7 (~ 3.8-5.0 invertebrate families/site) and lowest at sites 8, 1-2 (~ 2.0-2.85 invertebrate families/site; Figure 35a). Similarly, mean indices of diversity were highest ($p < 0.01$) at sites 3-6 (Hill's N2: ~ 7.7-11.1; Shannon Index: ~ 2.30-2.58) and lowest at sites 8, 1 and 2 (Hill's N2: ~ 3.3; Shannon Index: ~ 1.6; Figure 35a; b). Mean values of Pielou's Index of evenness per sample site had the same patterns as diversity indices (highest at sites 3-7: ~ 0.77-0.85; lowest at sites 8, 1and 2: ~ 0.15-0.31; Figure 35c). Conversely, mean dominance index (Simpson) was lowest at sites 3-7 (~ 0.14-0.21) and highest at sites 8, 1-2 (~ 0.41-0.55; Figure 35d).

Assemblage Classification and Ordination

A cluster analysis (using realtive Euclidean distances and a flexible strategy with $\beta = -0.25$) of the macroinvertebrate assemblages was similar to those constructed for the helminth component community data (Figure 36a). The two main cluster groups defined were: (i) sites 4-6 and (ii) sites 8, 1, 2, 7 and 3. (Note that previously sites 3 and 7 were

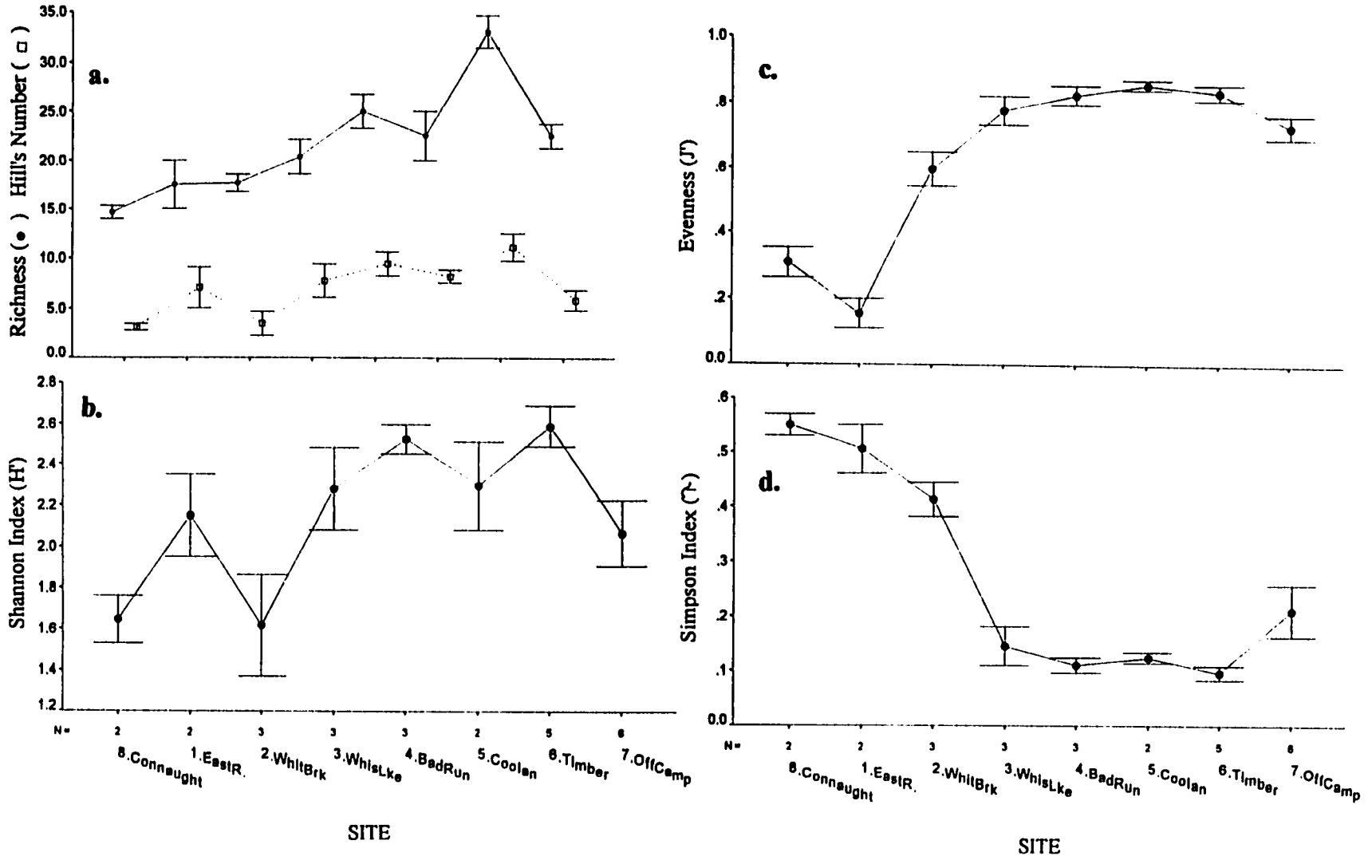


Figure 35. Mean (± s.e.) ecological indices :(a.) Richness (S) and Hill's Number (N2); (b.) Shannon Index (H'); (c.) Pielou's Index of Evenness (J') and (d.) Simpson Index (λ) for benthic stream macroinvertebrate assemblages at each site during August 1996.

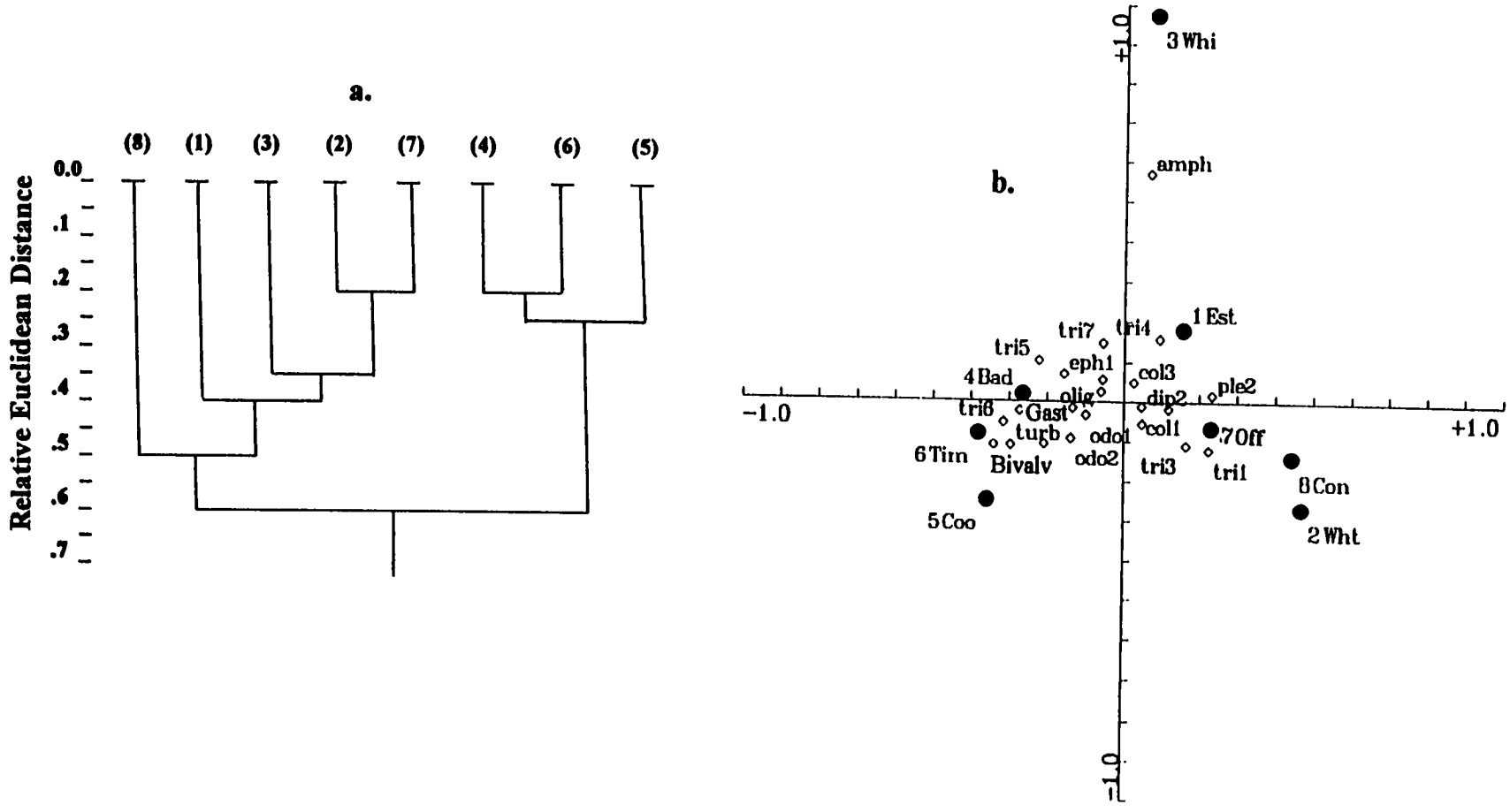


Figure 36. Results of : (a.) cluster analysis using relative Euclidean distances and the flexible strategy (β = -0.25) and (b.) correspondence ordination for the benthic stream macroinvertebrate assemblages collected in August 1996. (Numbers in parentheses refer to site numbers as per Figure 1.)

(Sample sites denoted by (●); several invertebrate taxa labels omitted for clarity)

clustered with group (i) when using helminth community data.)

Results of correspondence ordination on the same data (Figure 36b), produced similar results to the cluster classification: sites 4-6 were placed on a different side of the axes than sites 1-3, 7 and 8. Components 1 and 2 accounted for 52 % of the variation in ordination scores among sample sites. The ordination of sites 1, 2, 7 and 8 were determined by the abundance of : (i) Hydropsychidae, Polycentropodidae and Lepidostomatidae (Trichoptera); (ii) Chironomidae (Diptera) and (iii) Gyrinidae and Dryopidae (Coleoptera) while the ordination of site 3 was determined by the abundance of Gammaridae (Amphipoda). Sites 4-6, having the highest richness, were positioned on the abundance of several invertebrate taxa, predominantly: (i) Sphaeridae (Bivalvia); (ii) Gastropoda; (iii) Heptageniidae and Baetidae (Ephemeroptera); (iv) Helicopsychidae, Hydroptilidae and Leptoceridae (Trichoptera); (v)Tabanidae (Diptera) and (vi) Turbellaria.

Multiple linear regression analysis of the ordination axis on the environmental variables pH, flow rate and distance from sea resulted in pH being the only factor significantly ($r^2 = 0.909$, $p < 0.01$) related to the ordination scores of each sample site along axis 1. The percentage contibution of pH explaining the variation in sample site ordination scores along axis 1 was 98.6 %. No other significant relationships existed among the remaining environmental variables and ordination scores of the sample sites.

4. DISCUSSION

Parasite ecologists have often searched for 'structuring' processes of helminth communities among patterns observed in the 'final result' - the collection within the definitive host. When reviewing the literature on parasite communities of fishes, one gets the impression many studies were approached with an *a priori* assumption that the 'structure' was a function of the parasites themselves. Seldom have such studies addressed the influence of host biology (both definitive and intermediate hosts) as a possible structuring determinant, which seems ironic, considering most studies apply to intestinal helminths. The trans-mission of these parasites is by ingestion, yet few studies of parasite community ecology acknowledge the importance of host diet and the structure of food webs.

In the present study, if sampling methods were size biased (e.g. only used pots, thus caught all eels over 40 cm, or, only sampled habitats where eels < 20 cm), different results would have been observed and, consequentially, much different conclusions would have been made. Before any discussion of parasite communities in *Anguilla rostrata* can be attempted, it is necessary to review several patterns in eel biology from the present study, and how these could contribute to the observed patterns in community structure.

4.1 Eel Biology

Catch Statistics

Variation in eel density and CPUE among sample sites may have been the result of sampling methods rather than localized eel dispersion. Daily weather fluctuations (e.g.

rainfall, low temperature, high winds) were often followed by low CPUE values. At sites 3 and 5-8, the lake mouths and adjacent shoreline would be electrofished. At times of spates or excessive dry periods, the actual area that could be sampled would be altered, such that it was impossible to catch eels that may have moved only 3-4 metres from the 'electrofished zone' into deeper water. Eel density estimates based on data supplied by DFO at the same sample sites in July during 1995 and 1996 were generally 5 to10 times higher than those I obtained. Their sampling team consisted of 4-6 people and they used 'barrier nets' to isolate a fishing zone. In contrast, 90% of electrofishing in the present study was conducted by one person (carrying both electrofisher and collecting net). It is unlikely any of these sites were over-fished (by my methods), thereby altering eel population structure and, consequentially, parasite prevalence.

Despite the 'inefficiences' of sampling, there was an overall trend at all sites for CPUE to increase in June and July, possibly a consequence of increased water temperature. Walsh *et al.* (1983) reported an increase in activity of *A. rostrata* at temperatures above 12°C, and a decrease in activity below 7°C. In the present study, if the water temperature at any sample site was 7°C or less, it was impossible to catch any eels. Similarly, Jellyman (1991) reported a high positive correlation between CPUE and water temperature when collecting longfinned eels, *A. dieffenbachii*, in New Zealand.

Sites 2 and 6 had significant monthly peaks in eel density and CPUE during June and July, respectively, during 1995 and 1996. These peaks were a result of dense aggregations of small eels (8-15 cm) at these sites. Dutil *et al.* (1989) recorded a similar pattern in Quebec, where they noted elvers (< 8 cm) did not migrate further than 4 km

upstream in their initial year in freshwater. In their second year, these same juvenile eels began another upstream migration, this time extending to the upper reaches (> 15 km) of the catchment. This 'second migration' pulse coincided with the arrival of new elvers migrating upstream from the estuary. In a similar study, Moriarity (1986) reported the same patterns, concluding upstream migration by small, juvenile eels (< 15 cm) may be influenced by population pressure at the lower reaches of a river. In the present study, eels as small as 8.5 cm were caught in dense aggregations of juveniles at site 6 (during July 1995 and 1996), located 19 km from sea. This could be a reflection of the previously described 'second migration' of juvenile eels within a freshwater catchment.

At site 1, peaks in eel density and CPUE occurred in September, which was a result of aggregations of seaward-bound maturing silver eels. The high percentage of males (~ 81-85%) among the sample of silver eels is inconsistent with the theories: (i) latitudinal sex ratio - more males at lower latitudes (Tesch, 1977; Pennisi, 1989) and (ii) males prefer estuarine habitats (Bigelow and Schroeder, 1953; Vladykov, 1966, cited in Jessop, 1987); furthermore, it is inconsistent with the sex ratios of silver eels in three nearby rivers in Nova Scotia (Jessop, 1987). Misidentification of the silver eels as male or female may not have been a factor as the patterns in length relationships and sexual dimorphism (eye size) were consistent with other studies of both *A. rostrata* (Winn *et al.*, 1975; Gray and Andrews, 1970; Jessop, 1987) and *A. anguilla* (Vøllestad, 1992; Poole and Reynolds, 1996; Svedäng *et al.*, 1996). Jessop (1987) reported that silver males migrate earlier than silver females, thus, it is possible my sampling protocol 'missed' the run of females. Furthermore, Jessop (1987) used fyke nets set overnight, while all silver

eels in the present study were collected by electrofishing during daylight.

Overall, the data indicate there may be two types of migration occurring within the catchment: (i) upstream migration of elvers and small eels (< 15 cm) in June and July, and (ii) the downstream seaward migration of sexually maturing silver eels from July to October.

Length and Body Somatic Indices

Eel length and population density were similar throughout the watershed and did not vary with distance from sea. However, studies using *A. anguilla* in England reported a decrease in eel density and increase in eel size as distance from sea increased (Barak and Mason, 1992). Similar results have been reported for *A. japonica* in Japan (Tzeng *et al.*, 1995). In the present study, the only distinct relationship with eel size was that larger eels (> 35 cm) were most common in deeper water (> 1 m), as evidenced by the large eels caught in pots. Interestingly, the eels at the upper reaches of the limed portion of the watershed (sites 6 and 7, 19 and 22.5 km from sea, respectively) were the smallest, while those from the most acidic regions of the watershed (sites 8 and 1, 8.5 and 1 km from the sea, respectively) were the largest among all electrofished eels.

Condition factor significantly increased and HSI significantly decreased with increasing eel length. The observed differences in condition factor and hepatosomatic index (HSI) from site to site and between parasitized and non-parasitized eels may have been a consequence of eel size rather than eel health. Jessop (1987) reported higher condition factors for *A. rostrata* than those in the present study, and consequently, these were larger eels. Many studies have used body somatic indices as valid indicators of

impaired health among fish populations (see reviews in Adams, 1990 and Servos *et al.*, 1996), but the somatic index results of the present study do not indicate any such health impairment associated with either habitat and/or pathology of parasites.

The present results of visceralsomatic indices (VSI) indicate eels do most feeding in May, then reduce the amount consumed over summer. This trend was also refected by an increase in the number of empty stomachs among eels collected from May to October. Similar results were reported for *A. rostrata* by Barak and Mason (1992) and for *A. dieffenbachii* by Jellyman (1989). The observed increase in frequency of eels with empty stomachs as temperature increased may also be a result of faster rates of digestion at elevated temperatures. Jellyman (1989) noted digestion rates for wild populations of *A. dieffenbachii* to have a range of 24-36 hours. Small (< 10 cm) and large (> 45 cm) eels in the present study had the highest VSI, but the high value for small eels is questionable. Given the limited precision (0.1 g) of the scale used to weigh the eels' stomachs, any excess fluid associated with the stomachs of these small eels could account for considerable error, thereby artificially increasing VSI. Silver eels had the lowest VSI of any sample and their stomachs were beginning to degenerate, consistent with the theory that silver eels cease feeding prior to migration (Tesch, 1977). Pankhurst and Sorensen (1984) reported similar low VSI values and degenerate gastrointestinal systems among *A. rostrata* and *A. anguilla* silver eels.

Age Analysis

Many studies on ageing eels debate the validity of using otoliths due to the presence of supernumary ('false') annuli (Moriarity, 1983; Berg, 1985; Vøllestad, 1985;

Michaud *et al.*, 1988). Despite such variation, both techniques used in the present study were well supported by statistically significant linear models. Vøllestad (1985) also noted that the alcohol clearing technique predicted 'lower' ages for eels than did the traditional 'burning and cracking' method. In the present study, the toluidine blue staining technique by Richter and McDermott (1990) was more appropriate (and reliable) for several reasons : (i) it was difficult to distinguish the annuli of many large otoliths cleared in alcohol; (ii) some otoliths simply would not clear in alcohol; (iii) some otoliths cleared excessively and (iv) stained otoliths had distinct annuli.

The predicted eel ages in this study, based on the toluidine blue staining technique, agree with previously reported age data of *A. rostrata* from Nova Scotia (Jessop, 1987) and Newfoundland (Gray and Andrews, 1971). Thus, eels in Nova Scotia appear to be a long lived fish (up to 30-40 years in freshwater). Additionally, many studies suggest sexual maturity (silvering) in eels is more specifically related to eel size rather than eel age (Vøllestad, 1992; Poole and Reynolds, 1996; Svedäng *et al.*, 1996).

Eel Diet

Despite an overall varied diet (~ 13+ prey types), the data indicate feeding specialization (monophagy) by individual eels among (and within) different sample sites. Small eels (< 15cm) fed exclusively on Amphipoda and Diptera (Chironomidae and Simulidae), whereas larger eels (> 40cm) tended toward piscivory. These dietary trends were illustrated in various ecological indices, whereby the lowest prey diversity and highest prey dominance was found in small and large eels.

Site to site variability in prey consumed presumably reflected the local composition

of the benthic macroinvertebrate assemblage. At the sites of lowest pH (8, 1, 2), the prey assemblage consumed was characterized by low diversity and high dominance, whereas the reverse dietary patterns were observed among the diet of eels from sites of higher pH (3-7). Absence of molluscs and amphipods from the diet of eels at the low pH sites was most likely the result of an absence of these species from the local macroinvertebrate assemblage as both groups have been reported to have many acid-sensitive species (Hynes, 1970; Roff and Kwiatkowski, 1977; Rooke and Mackie, 1984; Sutcliffe and Hildrew, 1989; Muniz, 1991; Schindler *et al.*, 1991).

Results of the modified Costello (1990) method indicated individual prey types were consumed in a high frequency by individual eels, but, most prey items were represented by a limited proportion of the population at any sample site. It appeared as if many eels were specializing on certain prey types (monophagy). Further evidence of feeding specialization in the present study was evident in the frequency of the number of different prey types found in each eel. Most eels (~ 85 %) were recorded with only one prey type (i.e. Trichoptera) in their stomach. Less than 10% of all eels in the present study had more than 2 types of prey, and the maximum number of prey in any eel was 5. When several types of prey were found in an eel, all prey items were in unequal amounts, one type would dominate.

Similar prey taxa were reported for populations of *A. rostrata* in the Chesapeake Bay area (Ogden, 1970; Wenner and Musick, 1975; Facey and LaBar, 1981; Denoncourt and Stauffer, 1993). Tesch (1977) noted that dietary niche breadth was least in small eels (<15cm) while Ephemeroptera and Trichoptera were common prey items of larger *A.*

rostrata and *A. anguilla*. Dutil *et al.* (1989) reported a high occurrence of Chironomidae (Diptera) among small eels (< 15 cm) and little or no food among eels less than 8 cm that were migrating upstream. Piscivory in larger eels (> 40 cm) has been reported for populations of *A. rostrata* from the eastern United States (Facey and LaBar, 1981; Denoncourt and Stauffer, 1993), *A. anguilla* from Israel and England (Golani *et al.*, 1988; Barak and Mason, 1992), and *A. australis* and *A. deiffenbachii* from New Zealand (Jellyman, 1989; 1996). Jellyman (1989) further commented that there was some evidence of feeding selectivity and monophagy and changes in diet with size among populations of *A. australis* and *A. deiffenbachii*.

Traditionally, eels have been described as opportunistic feeders, consuming a wide variety of prey types (Scott and Crossman, 1973; Tesch, 1977), but the present data indicate feeding specialization by many individuals of the population. When local 'blooms' occurred (e.g. abundance of Ephemeroptera naiads in May and Simulidae larvae in September), most eels were consuming the same prey. Such results support the idea of opportunistic foraging - eels were consuming the most locally abundant prey. In addition, some eels had consumed terrestrial prey (e.g. spiders, caterpillars which had presumably fallen from trees along the stream border), a further indication of opportunism. Site to site habitat heterogeneity may have accounted for some of the dietary specialization observed between eels from different sites (e.g. Plecoptera were most abundant at sites of high stream flow). However, within each site, differences in eel size accounted for dietary specialization (monophagy) among individuals of the local population.

Mark-Recapture Study

Results from the mark-recapture study suggest site fidelity among eels greater than 16 cm living at the various sample sites of this watershed. No tagged eel was ever captured at a different site from where it was initially caught and tagged during a period of over 2 years. Recapture percentages (~ 8-15%) were consistent (during 1995 - 1997) and similar among sample sites. The values reported in the present study were comparable to recapture percentages (using same type of tags) for studies on *A. rostrata* in Canada and the United States (Hurley, 1972; Helfman *et al.*, 1984 respectively), *A. anguilla* in England (Dekker, 1989) and *A. australis* in New Zealand (Jellyman *et al.*, 1996). The frequently recaptured eels appeared to be microhabitat specific, as most were caught within 1-2 metres of the same area of stream (e.g. large boulder or macrophyte bed). The sedentary nature and strong degree of site fidelity of eels may have contibuted to dietary specialization, as eels may only be feeding within their home range ('activity region'). After tagging, some eels were not recaptured until several months to over a year later. This may simply have been an artifact of the previously described 'ineffecient' electrofishing technique - these eels were possibly only 2-3 metres outside the fishing zone, in water too deep to sample. The low mean recapture times at site 1 may have been a result of limited residency time by the eels or it may have been a reflection of the difficulty of sampling that site..

Discarded tags and mortality of tagged eels could have reduced success of tag returns. Only 10 eels were recaptured with tag scars, 8 of which initially had the fingerling tags sewn through the dorsal skin. Mortality rates were not estimated, but the few dead

tagged eels that were recovered were observed near the initial site of release at times of high water temperature. Their deaths were likely a combination of stress during handling and low oxygen content in the water. One tag was found in the stomach of a large eel, but it is unclear whether this eel preyed upon another or simply ingested a discarded tag. Presumably, the burrowing nature of eels would help minimize predation by piscivorous birds on tagged eels. Dekker (1989) reported low retention times and high mortality among populations of *A. anguilla* tagged with floy tags. Several eels in this study were recaptured after 2 years, and all those recaptured with anchor tags showed no signs of inflammation or infection near the point of tag insertion.

There was no evidence of pot avoidance among tagged eels trapped in pots, as this sampling method had the highest percentage return. Perhaps the eels were actually attracted to the pots and were becoming accustomed to an 'easy meal' (one eel was caught 6 times in the same pot). Dekker (1989) reported no evidence of trap avoidance by tagged *A. anguilla* populations from several lakes in England. In the present study, several large eels (> 40 cm) initially caught by electrofishing in shallow water, were subsequentially recaptured in pots. This could be indicative of larger eels having a larger home range.

Homing ability was observed in 4 of 30 transplanted eels and this may be further evidence of site fidelity. (More transplanted eels had probably returned, but were not recaptured.) The size of the home range or the time taken to 'home' was of little importance to this study, as the main objective was an assessment of the existence and degree of site fidelity demonstrated by eels within the watershed.

Several species of eel (*A. rostrata, A. anguilla, A. dieffenbachii* and *A. australis*)

have been described as sedentary with home ranges varying between less than 50 to 300 meters, based on both telemetry (Helfman *et al.*, 1983; LaBar and Facey, 1983; Dutil *et al.*, 1988; McGovern and McCarthy, 1992; Jellyman *et al.*, 1996) and mark-recapture studies (Hurley, 1972; Boezman *et al.*, 1985; Dekker, 1989; Chisnall and Kalish, 1993; Jellyman *et al.*, 1996). Parker (1995) reported the largest home range (~2-12 km), using telemetry, but these were estuarine eels from a tidally influenced habitat. Parker (1995) suggested homing ability in eels is more precise than was once believed, and it is not just a return to a general hydrographic area, but rather to a specific substrate zone and it can occur quickly (e.g. within hours). Studies on *A. rostrata* and *A. anguilla* indicate most eel activity occurs at night, prior to sunset and shortly before sunrise (Dutil *et al.*, 1988; McGovern and McCarthy, 1992; Parker, 1995).

Jellyman (1977) reported limited movement among populations of *A. dieffenbachii* after several years of upstream migration as juveniles. The mark-recapture and population estimate data from this watershed support this trend. Eels in their first and second years in freshwater showed a widespread upstream dispersal, after which they establish localized site residency lasting from 15-30+ years when the maturing process begins (silvering) and eels commence downstream seaward migration. It is during the residency period that populations of *A. rostrata* in the present study acquire metazoan parasites.

4.2 Infracommunity

Patterns of Species Richness

The frequency distribution of the number of intestinal helminth species per eel in

the present study was comparable to published data on *A. anguilla* from the United Kingdom (Kennedy, 1990; 1993; 1995). However, the maximum number of intestinal helminth species in any eel was higher in *A. rostrata* than in *A. anguilla* (6 species c.f. 4 species) and was similar to values reported for Australian eels, *Anguilla reinhardtii*, (Kennedy, 1995). As length of *A. rostrata* increased, the proportion of eels devoid of parasites decreased. Furthermore, the frequency distributions of the number of both intestinal helminth species per eel and number of all metazoan parasite species per eel for samples of large *A. rostrata* (> 45 cm) in the present study were similar to that reported for *A. reinhardtii* (Kennedy, 1995), with few eels 'parasite-free' (~ 5-15%). If large specimens of *A. rostrata* lacked intestinal helminths, most (>95%) would harbour at least one species of gill parasite. Kennedy and Guegan (1996) reported only 3 of 2451 (0.12%) eels (*A. anguilla*) had more than 3 species of intestinal helminths. By comparison 24 of 2070 (1.15%) eels in the present study had more than 3 species of intestinal helminths. Both values are low, and most infested eels had only 1 or 2 intestinal helminth species, supporting the previous description of helminth infracommunities in eels as 'species poor' (Kennedy, 1990; 1993). In the present study, there may exist a link between monophagy and the low numbers of helminth species per eel. Recall that the frequency distribution of the numbers of intestinal helminth species per eel (Figure 15 a; b) was almost identical to the frequency distribution of the number of different prey types in the eel diet (Appendix A7-a) in 1995 and 1996.

Contrary to published data on *A. anguilla*, the mean helminth infracommunity richness and helminth infracommunity population of *A. rostrata* in the present study

increased with eel length such that the highest values of mean richness (~ 1.90-2.13 species/eel for eels > 45cm) were higher than those reported for *A. anguilla* (0.72-1.53 species/eel) but were within the lower range reported for *A. reinhardtii* (1.30-3.57 species/eel for eels 40-80cm; Kennedy, 1995). Marcogliese and Cone (1997a) reported lower values of mean infracommunity richness (0.49-1.49 species/eel) for *A. rostrata* sampled at various locations across Nova Scotia - values that were lower than those reported for *A. anguilla*. The data set by Marcogliese and Cone (1997a) was composed primarily of eels less than 35 cm, and lacked the same proportion of large eels (> 45cm) as used in the present study. Kennedy (1990) found no significant relationship between size of eel and infracommunity richness in *A. anguilla*, but the majority of these eels were also less than 35 cm. In the present study, there was little difference in helminth infracommunity richness among eels less than 25 cm. The observed increase in helminth richness associated with increasing eel size may be a combination of physical (available space in intestine) and biological (eel diet) factors. The largest eels, although exhibiting monophagy (piscivory) were consuming fish (e.g. *Catostomus commersoni, Fundulus diaphanus, Luxilus (=Notropis) cornutus*) that serve as transport host for several parasites: *Azygia longa, Bothriocephalus claviceps, Proteocephalus macrocephalus, Pomphorhynchus bulbocolli, Neoechinorhynchus rutili, Echinorhynchus salmonis* and *Eustrongylides* sp. (Lawrence, 1970; Cooper *et al.*, 1978; Muzzall and Bullock, 1978; Muzzall, 1980; Bursey, 1982; Weisberg *et al.*, 1986; Lassiere and Crompton, 1988; Measures, 1988; Arai, 1989; Cone *et al.* 1993). The remaining eels also displayed monophagy, but were consuming macroinvertebrates, any of which (source hosts) were

likely to be harbouring an infective stage of only one parasite species. Over 90% of small eels (< 10 cm) were 'parasite-free', consistent with the theory that these eels in their first and second years in freshwater are migrating ('dispersing') upstream and seldom feeding on benthic macroinvertebrates. It is not until their third year in freshwater (~ 11-15 cm), when they commence localized residency and begin to acquire metazoan parasites.

From site to site, the trend of increasing helminth infracommunity richness was evident except at the sites of lowest pH (sites 8, 1, 2). Since the diet of these eels was characterized by high dominance and low diversity, it is possible the low infracommunity richness was a reflection of the low numbers of available intermediate hosts, hence, parasite species available for colonization. Within a given site of higher pH (sites 3-7), the helminth infracommunity richness increased with size. It is likely that many macroinvertebrate hosts (thus parasite species) were available for colonization. There were no significant differences in mean helminth infracommunity richness for each eel size class when compared against the 8 sample sites for all size classes up to 35 cm. For example, regardless of where the eels resided, all eels of size class 15-20 cm had the same mean infracommunity richness. For each size class larger than 35 cm, significantly higher mean values of infracommunity richness were observed at the sites of greatest pH (sites 3-7). Site fidelity may have contributed to the observed differences in mean infracommunity richness among the same size class of eels at different sites, if there was a lack of mixing among adjacent populations. Interestingly, the eels collected in pots (from sites 3 and 5) had significantly higher values of mean intestinal infracommunity richness and mean total parasite assemblage richness than smaller electrofished eels at these same sites. This was

most likely a result of size (piscivory diet). It is unclear if the potted eels acquired additional parasites from ingesting bait, but large (> 45 cm) eels caught by electrofishing had similar high values of infracommunity richness as those eels colected in pots. Conneely and McCarthy (1986) reported high richness and diversity among lacustrine, compared with riverine, samples of *A. anguilla* within the same catchment, which they attributed to piscivory.

The silver eels collected at site 1 had significantly higher mean values of helminth infracommunity richness and total parasite assemblage richness than yellow eels (of the same size range) at site 1. Furthermore, the silver eels harboured intestinal species never found among yellow eels at site 1 (*A. longa, C. brevivitellum, P. bulbocolli*) and both species of gill parasites were present in higher abundances. Based on parasite fauna, it would appear these silver eels were not living at site 1 prior to commencing seaward migration.

Infracommunity Composition

Any one of 6 common intestinal helminths (4 of which were specialists) could dominate the infracommunity of *A. rostrata*. The majority of infracommunities (~ 50%) were dominated by the specialist nematode, *P. tenerrima*. Two species of digenes (1 specialist, 1 generalist) and one acanthocephalan generalist, *P. bulbocolli*, dominated a similar proportion of infracommunities (~ 10-15%). Among the larger eels (45+ cm), an additional 2 uncommon generalist species (*N. rutili*, *Eustrongylides* sp.) dominated less than 5 % of their infracommunities. All dominant species were autogenic except

Eustrongylides sp. (allogenic). The patterns of infracommunity composition for large *A. rostrata* in the present study differ from those reported for *A. anguilla* in which generalists (usually acanthocephalans) dominate most infracommunities (Kennedy, 1993); but, were similar for patterns in samples of *A. reinhardtii* in which nematode and digene specialists dominate most infracommunities (Kennedy, 1995). Furthermore, *Eustrongylides* sp. was not a dominant helminth among any infracommunities in *A. anguilla*, but dominated several infracommunities of *A. reinhardtii* (Kennedy, 1995). Kennedy and Bush (1994) reported that specialists that form a large proportion of a parasite community are indicative of a long period of co-evolution between parasite and host, thus the community has a strong phylogenetic component, and is characteristic of hosts in their 'heartlands'. It is possible the observed differences in infracommunity composition between *A. rostrata* and *A. anguilla* were simply a result of 'supply side ecology' (a consequence of more fish host species in the United Kingdom - 'flooding' the system with generalists).

Differences in the composition of helminth infracommunity of *A. rostrata* were observed among size classes and sample sites. Most infracommunities of smaller eels (< 25 cm) were dominated by either *P. tenerrima* or *P. bulbocolli*, with the highest percentages among eels less than 15 cm. In the largest eels (45+ cm), digenes (*C. brevivitellum*, *A. longa*) dominated most infracommunities while the remaining species dominated a similar proportion of infracommunities. The high dominance of *P. tenerrima* or *P. bulbocolli* among small eels is likely a consequence of diet specialization (Amphipoda, Chironomidae). Amphipods are required intermediate hosts for acanthocephalans (Arai, 1989; Gleason, 1989) and chironomids have been suggested as a possible intermediate

host for *P. tenerrima* based on laboratory experiments (C. Bartlett, pers. comm.). Both amphipods and chironomids decrease in percent occurrence among diet of larger size classes of eels and the percentage of infracommunities dominated by *P. tenerrima* or *P. bulbocolli* show a concomitant decrease. Similarly, the high percntage of digenes and relative 'even' representation of remaining species dominating the infracommunities of large eels may be indicative of piscivory. Among sample sites, differences in composition of helminth infracommunities (as with helminth infracommunity richness) was likely a product of local macroinvertebrate assemblages available as 'source' hosts. The infracommunities of eels at sites of lowest pH (sites 8, 1, 2) had few species (2-3) and were characterized by a high dominance of *P. tenerrima* (~ 77-90%). At the sites of highest pH (sites 3-7), the helminth infracommunities contained more species (6-8) with a more even dispersion - less dominance by *P. tenerrima* and most infracommunities dominated by digenes (~16-40%).

Why do most eels have only 1 or 2 species of intestinal helminths, despite having a potential maximum intestinal helminth infracommunity richness of 4 (or higher) species ? Among electrofished samples of *A. rostrata*, combinations of parasites of similar feeding guilds (e.g. absorbers - cestode and acanthocephalan) or common taxa were rare to absent, while among large potted eels, such combinations were slightly more abundant, perhaps implying physical space (availability of niches) as some 'limiting factor'. Alternatively, these differences may be a reflection of the relative abundances of these helminths within the catchment. Both species of cestode were relatively rare, thus it would be unlikely to see many combinations of acanthocephalans and cestodes. One interesting

trend was observed among eels infested with *B. claviceps*. Gravid specimens only occurred singly. When several specimens of *B. claviceps* were present, all cestodes were immature. Nie and Kennedy (1992) reported the same trend for *B. claviceps* infesting *A. anguilla*. Similar evidence of possible 'density-dependent' interaction was reported for the site selection of tapeworm (*Eubothrium crassum*) plerocercoid larvae in brown trout, *Salmo trutta* (Kennedy, 1996). The plerocercoids which established in the 'anterior' caecae of the stomach (the preferred site) were able to mature, while those located in the posterior caecae failed to attain maturity. Density dependent intraspecific competition was confined to the early, post-invasive period when larvae were migrating to the caecae. Kennedy and Moriarity (1987) and Kennedy (1992) reported a high percentage of infracommunities of *A. anguilla* dominated by common guild members and congeners, with little evidence of any interaction. Furthermore, Conneely and McCarthy (1986) also could not find any evidence of interaction among combinations of intestinal helminths in populations of *A. anguilla*, concluding that the observed combinations were more a result of local helminth distribution.

Tests of association (based on presence / absence data) among the helminth infracommunities of potted eels were not significant during 1995 and 1996, implying that all helminths occurred independently of one another in these large eels. However, tests of association among helminth infracommunities of electrofished eels were significant during 1995 and 1996, implying that all species did not occur independently of each other. The presence of *P. tenerrima* was negatively associated with each species of intestinal helminths during 1995 and 1996. Tests of covariance (based on helminth abundance data)

were not significant among either electrofished or potted eels during 1995. In 1996, the abundances of *P. bulbocolli* and *P. macrocephalus* were positively correlated among electrofished and potted eels, implying both abundances increased concurrently. Perhaps both parasites use the same intermediate host or were both abundant at a particular sample site. Among electrofished eels only, there was also a significant positive correlation in the abundances of *P. tenerrima* and *P. bulbocolli* which was probably a by-product of the high dominance of these two species in the infracommunities of eels smaller than 25 cm. The only significant negative correlation was observed between the 2 species of digenes, implying as the abundance of one increased, the other decreased. It is unlikely competition exists between these species as they were located in different microhabitats within the eels (*C. brevivitellum* in upper intestine, *A. longa* in stomach). Both species use different molluscs as first intermediate hosts: (i) sphaerid clams for *C. brevivitellum*; (ii) amnicolid snails for *A. longa* (Cone *et al.*, 1993). It is possible the distribution of these (or other) intermediate hosts are negatively correlated due to habitat conditions (e.g. substrate, flow, vegetation).

Whether or not any of the observed significant differences in species-pair combinations provide evidence of interspecific competition within helminth infracommunities is equivocal. All observed differences can be explained by differences in diet specificity influencing infracommunity composition among size classes of eels and sample sites. The high percentage of eels with no parasites (> 50%) may be a reflection of diet specificity and limited mobility. Freshwater habitats show considerable species heterogeneity over limited distances (Hynes, 1970). Less than 10 species of invertebrates

are used as intermediate hosts for the parasites reported in the present study, but more than 50 species of invertebrates may be present at any sample site. Little data exist that provide good evidence of interspecific interactions between intestinal helminths of freshwater fishes. Experimental evidence of interference competition between 2 species of acanthocephalans (*Pomphorhynchus laevis* and *Acanthocephalus anguillae*) in rainbow trout, *Onchorhynchus mykiss*, has been reported, but, these same 2 helminths failed to show any evidence of interaction in experimentally infested eels, *A. anguilla* (Bates and Kennedy, 1991). Grey and Hayunga (1980) reported a shift in preferred site attachment (from posterior to anterior intestine) by *Glaridacris laruei* (Cestoidea) in the presence of acanthocephalan, *P. bulbocolli*, in samples of white suckers, *Catostomus commersoni*, but no inferences were made as to the role of such interaction in determining helminth community structure. Most data supporting inter- (and intra-) specific interactions (competitive or otherwise) have been from work on mammals and aquatic birds (Holmes, 1973; Holmes and Price, 1986; Holmes, 1990a), whose helminth infracommunities are often richer and more diverse than those of freshwater fishes (Kennedy *et al.*, 1986).

Overall, the intestinal helminth infracommunity data from *A. rostrata* support an extension of MacArthur and Wilson's (1963) 'island size' hypothesis. In the present study, island size pertains to host size and larger eels had more species of intestinal helminths and more individuals of each species. Guegan and Hugeny (1994) also concluded host size was the most important factor structuring infracommunities of monogeneans on the gills of tropical fish. No evidence could support (or refute) Holmes (1973) 'competition hypothesis', whereby inter- (and intra-) specific competition (past or present) plays a major

role in structuring helminth infracommunities. For these data, host biology (size, diet), a ontogenetic influence, plays a major role in determining the intestinal helminth infracommunity richness. However, local environmental factors (e.g. pH, availability of macroinvertebrate source hosts), an ecological component, were observed to influence composition of intestinal helminth infracommunity richness in *A. rostrata*.

4.3 Parasite Population Biology

The seasonal cycles for the parasites of *A. rostrata* in the present study were not clearly defined by peaks in prevalence and mean abundance. Most recruitment for all 8 species was from early July to late August. The parasites found in the present study have annual life cycles (Arai, 1989; Marcogliese *et al.*, 1990; Nie and Kennedy, 1991a; 1991b; 1991c; 1992; Hudson *et al.*, 1994). Thus, overlaps between generations were inevitable. It was quite interesting to see striking similarities between the parasite assemblage at any given site in October and that in the following May, implying most parasites were capable of 'overwintering' in (or on) the eels during torpor, when they are submerged in the substratum. Furthermore, in October, several species (*P. tenerrima, A. longa, C. brevivitellum, B. claviceps, P. anguillae*) were immature, but appeared in the following May as maturing or gravid. In a series of studies on the population biology of several helminths of *A. anguilla* in Britain, 'overwintering' was reported for *P. tenerrima, B. claviceps, P. macrocephalus* and *P. anguillae* (Nie and Kennedy, 1991a; 1991b; 1991c; 1992).

The 8 common parasites of *A. rostrata* in this watershed had patchy distributions

within the watershed. In addition, there were differences in prevalence and mean abundance associated with size of host and time of sample. It is likely the sedentary habits and limited mobility of eels among sample sites in this study contributed to maintaining the heterogeneity of the parasites' distributions. Several parasites were absent (or rare) at the sites of lowest pH (sites 8, 1, 2). The absence of both digenes and rarity of the acanthocephalan from these sites is likely a result of the acid-sensitivity of their molluscan and amphipod hosts, respectively. Marcogliese and Cone (1996) and Cone *et al.* (1993) reported a similar loss of digenes and acanthocephalans from eels collected at sites of pH < 5.4. Both species of gill parasites (*E. celestis* and *P. anguillae*) were absent from the site of lowest pH (site 8) and rare at site 1 and their abundances were positively correlated with pH and negatively correlated with flow rate. High flow rates would certainly pose a problem for the transmission of *E. celestis* nauplii and *P. anguillae* oncomiracidia. The gill monogene, *P. anguillae*, appeared to be more susceptible to flow rate, being most common at the sites of lowest flow, and further indicated by its significant decline from the watershed during the numerous spates of 1996. The spates must have affected dispersal, perhaps occurring at times of peak release of oncomiracidia. Eggs of *P. anguillae* are unable to hatch at temperatures below 10°C, and the optimum temperature range for hatching is 20-30°C (Buchmann *et al.*, 1987). This is consistent with the observed increases in prevalence and mean abundance of *P. anguillae* from May to August during 1995 and the 'loss' of the parasite after the first spate in July 1996. The apparent lack of any decrease in abundance of *E. celestis* during 1996 might be attributed to a continual production of nauplii from May to August (Hudson *et al.*, 1994), thereby overcoming any

unsuccessful transmission associated with spates. However, *E. celestis*, was never found at site 1 and 4 after the first spate of July 1996. Prior to the spates of 1996, it was rare at these sites of high flow.

The ubiquitous nematode, *P. tenerrima*, was the only abundant parasite at the sites of low pH. The life cycle is unknown for this species, but several suggestions include: (i) a monoxenous life cycle (Moravec, 1974, cited in Nie and Kennedy, 1991c); (ii) heteroxenous life cycle, involving a piscine host (Conneely and McCarthy, 1986); (iii) larval insect host (Nie and Kennedy, 1991c) and (iv) planktonic host (Kennedy *et al.*, 1992). The present data indicate, if an intermediate host is required, it must be tolerant of habitats of high water flow and low pH. Some appropriate groups are Chironomidae and several familes of Trichoptera - Hydropsychidae and Polycentropodidae (Hynes, 1970; Hilsenhoff, 1977). These taxa were also common prey items in the diet of eels from these same sites. Experimentally, chironomids have been demonstrated as a successful intermediate host (C. Bartlett, pers. Comm.) in the life cycle of *P. tenerrima*. There was little evidence in the present study to support the idea of either a piscine (high dominance of *P. tennerima* in very small eels) or planktonic (high flow rates) intermediate host.

Both gill parasites and the intestinal helminths *A. longa* and *P. macrocephalus* significantly increased with size of eel. In comparisons among sample sites, the potted eels had the highest values of prevalence and abundance for these species. Nie and Kennedy (1991a) and Hudson *et al.* (1994) both reported similar significant increases in prevalence and abundance of *P. anguillae* and *Ergasilus* spp., respectively. Obviously, larger eels have more spaces available on their gills for colonization and the abundance of larger eels

in deeper waters (low flow rate) facilitates colonization and transmission by these parasites. One peculiarity was observed with respect to concurrent infestations of *E. celestis* and *P. anguillae*: eels 45+ cm had very low prevalences and abundances of *P. anguillae*, their gills were dominated by *E. celestis* (often > 200 individuals/ host). It is unclear whether this was evidence of interspecific competitive exclusion or some reflection of difference in habitat. Rohde (1979) noted that monogenes are very site-selective, and display a high degree of host specificity. Occupancy of narrow niches was necessary for maintenance of intraspecific mating, and presence of other guild members had no effect as 'vacant niches' were abundant.

The increases in abundance and prevalence of *A. longa* among larger eels is likely attributed to piscivory as *A. longa* has been reported to use an optional piscine host (Cone *et al.*, 1993). Furthermore, specimens of *A. longa* were quite large (~ 15-30 mm long). It is possible the size of the eels' stomach may have been an additional factor contributing to successful colonization. Increases in prevalence and abundance of *P. macrocephalus* with eel length was also reported by Conneely and McCarthy (1986) and was attributed to piscivory. A copepod intermediate host is required, supporting the idea of plankton feeding by eels (Kennedy *et al.*, 1992); however, an optional piscine transport host has also been speculated (Cone *et al.*, 1993). The present data support the role of piscivory, as it is unlikely these vary large eels would consume plankton. Furthermore, the increased flow rates of 1996 did not alter the distribution of this parasite.

The prevalence and abundance of *P. bulbocolli and P. tenerrima* was also affected by eel size. The prevalence of *P. bulbocolli* was highest in both small and large eels. The

small eels were likely acquiring the parasite by ingestion of amphipods (which dominated their diet), whereas, large eels (45+ cm) were likely acquiring it through piscivory. Many acanthocephalans are capable of post-cyclic transmission (Lassiere and Crompton, 1988; Arai, 1989). A predator can acquire the parasite by ingesting an acanthocephalan-infested piscine host. The abundance of *P. bulbocolli* was low in small eels, presumably a function of size of the intestine (limited number of available 'preferred sites'), and it was in these eels (most < 20 cm) that many extra-intestinal, encapsulated specimens of *P. bulbocolli* were observed. The prevalence and abundance of *P. tenerrima* slightly increased with size, but it was unclear if this was a factor of diet or size of intestine. Conneely and McCarthy (1986) also reported an increase in prevalence and abundance of *P. tenerrima* in *A. anguilla* from Ireland, which they attributed to piscivory in larger eels.

Significant monthly peaks in prevalence and abundance were observed for two helminths: *P. tenerrima* (June) and *P. bulbocolli* (October). The peak in prevalence and abundance of *P. tenerrima* in June was indicative of its seasonal cycle. In June, over 90% of all specimens were gravid or sexually mature (spicules evident). In subsequent months, a rapid decline in prevalence and abundance was associated with death and loss of adults and new recruitment. Nie and Kennedy (1991c) described the same seasonality for *P. tenerrima* in *A. anguilla* in Britain, however the cycle there peaked slightly earlier (April - May). Conversely, the peak in prevalence and abundance of *P. bulbocolli* was somewhat artificial and can be attributed to supply-side ecology: a local abundance of intermediate and alternate definitive hosts. Very few specimens (< 5%) attained maturity. The development of the proboscis bulb and site of attachment was poor. Most specimens were

'wrinkled' (lacking plumpness) and many were found encapsualted extra-intestinally. These are all characteristics of an acanthocephalan being in a 'non-preferred' host (Kennedy, 1984; Conneely and McCarthy, 1986; Taraschewski, 1989). The increase in acquistion of these generalist parasites by eels in October was a result of them being locally abundant in amphipods and several fish species (*C. commersoni, L. cornutus*) at that time (Lawrence, 1970; Muzzall and Bullock, 1978; Muzzall, 1980). Based on the present study, perhaps the status of *P. bulbocolli* as a valid member of the intestinal helminth community of *A. rostrata* needs to be re-evaluated.

Some additional interesting trends were observed relating to the population biology of these helminths. First, the values of prevalence and abundance for *P. tenerrima, B. claviceps, P. macrocephalus* and *P. anguillae* reported in this study were lower than those reported for the same species infesting *A. anguilla* in Britain (Nie and Kennedy, 1991a; 1991b; 1991c; 1992). This might be related to the higher dominance (less evenness) observed among parasite component communities reported for *A. anguilla.* Second, for 6 of the 8 common metazoan parasites in the present study, there were no significant differences in intensity among different sample sites or among the different eel size classes, despite having significant differences in abundance and prevalence. Infested eels had the same mean number of parasites/eel, regardless of where they originated or how large they were. This suggests some type of 'ceiling effect' or saturation point, similar to the limit on infracommunity species richness per eel. Finally, there was an amazing consistency from 1995 to 1996 in the amount of parasites recovered (sums per site) and in their dispersion (prevalence, abundance). This suggests some type of underlying

structuring determinant, perhaps further evidence of phylogenetic influence.

4.4 Component Community

Spatiotemporal Composition

Most intestinal helminth component communities of *A. rostrata* were dominated by either of 2 specialists : *P. tenerrima* or *C. brevivitellum*. Only 5 species (3 of which were specialists) of intestinal helminths (of a possible 9) dominated the component community. As with composition of the infracommunity, these patterns are more similar to the component communities of *A. reinhardtii* in Australia as opposed to its sister species, *A. anguilla* in the United Kingdom (Kennedy, 1995). The composition of the component community was dynamic in spatiotemporal variation in the dominant helminth species per month and per sample site. At the sites of lowest pH (Sites 8, 1), *P. tenerrima* dominated every component community during each sampling month of 1995 and 1996. At the sites of higher pH (sites 3-7), *P. tenerrima* only dominated component communities from May to July of 1995 and 1996. From August to October, component communities at these sites would be usually dominated by either species of digene or the acanthocephalan, *P. bulbocolli*. Such spatiotemporal variation was a result of a combination of parasite life cycles and probably seasonality of macroinvertebrate assemblages whose members were serving as intermediate or transport hosts. The observed seasonal and site variation in component community composition emphasizes the limitations of parasite community studies based on single samples at one time of the year. For example, within this watershed, sampling at different times of the year could produce misleading results: (i) if

site 1 was sampled from May to July, the component community would appear species poor and dominated by a nematode, but, if site 1 was sampled from August to October (thereby catching a high proportion of seaward migrating silver eels), the component community would appear species rich, and dominated by digenes; (ii) if any site of high pH was sampled in June, the component community would be charcterized by a high dominance of *P. tenerrima* (peak reproductive period), but, sampling any of these high pH sites in August would result in component communities characterized by low dominace, high eveness (low abundances of *P. tenerrima*). In addition, if the component communities of eels living at headwaters of catchments were sampled and compared with those at lower reaches (nearest ocean), sampling at site 6 or 8 in this watershed would result in two completely different conclusions (species rich or species poor). Cone *et al.* (1993) examined the metazoan component communities from *A. rostrata* at sites 1, 4 and 8 during July or August of 1989 - 1991 and noted inconsistent prevalence and intensity values for *P. tenerrima*. July and August is a post-reproductive period for *P. tenerrima*, a time when most adults die after mating, accounting for 'aberrant' abundances. Thus, caution should be addressed when making conclusions from data that are 'snapshots' in time of a seasonally dynamic helminth community.

Component Community - Diversity and pH

The ecological indices describe the intestinal helminth component communities at the sites of low pH (sites 8, 1, 2) as having low species richness, low species diversity and high dominance during 1995 and 1996. The opposite trends were observed at the sites of

higher pH (sites 3-7): high richness and diversity, low dominance. The pattern of increased helminth component community diversity and richness at higher pH levels observed in this watershed was paralleled on a regional scale (across Nova Scotia), and the mean values reported for diversity (H', N2, mean species richness) within this watershed were identical to those reported across Nova Scotia for the same pH range (Marcogliese and Cone, 1996). At the sites of highest pH within the watershed, helminth component community diversity indices (H', N2) for samples of *A. rostrata* were higher than those reported for *A. anguilla* in the United Kingdom and were within the range reported for *A. reinhardtii* from Australia (Kennedy, 1990; 1993; 1995). Similarly, the dominance indices in these same component communities from *A. rostrata* were much lower than those reported for *A. anguilla* in the United Kingdom and within the range reported for *A. reinhardtii* in Australia (Kennedy, 1990; 1993; 1995). Thus, helminth component communities (among eels living at high pH habitats) of *A. rostrata* are characterized as being more diverse, with a more 'even' represenatation of species, than those of *A. anguilla.* This is somewhat confounding, as component communities of eels in the United Kingdom have a suite of 22 'available' species (Kennedy 1990; 1993), whereas those of Nova Scotia have 12 species (Marcogliese and Cone, 1996; Barker *et al.* 1996).

Results of cluster analyses on the helminth component community data (using species abundance data) identified two main groups ('clusters') that could be characterized by pH: (i) pH < 5.4, sites 1, 2 and 8; (ii) pH > 5.4, sites 3-7. An additional cluster analysis, using ecological indices (species richness, H', N2, λ, J'), produced similar groups, with the only exception of site 7 now being included with the low pH group. Site 7 was somewhat

atypical as it received annual liming, but is located in an acidic peat bog, thus its pH declined over summer. Silver eels (>95% caught at site 1) when treated as a 'sample site', clustered with sites 3 and 5 during 1995 and 1996, further evidence that these silver eels were not residents of site 1, prior to commencing seaward migration.

Several ordination procedures were initially applied to the helminth component community data (Bray-Curtis polar ordination, principle components analysis, correspondence analysis and detrended correspondence analysis) and all produced similar results. However, correspondence analysis (CA) was chosen as the most applicable for this data, as it assumes non-linearity of the data (e.g. species abundances respond to some environmental gradient in a unimodal relationship) and calculates weighted covariance matrices (eigen values) based on species-species and site-site differences (Ludwig and Reynolds, 1988; Jongman *et al.*, 1995). The CA ordination plots for both 1995 and 1996 are very similar and depict the relative influence of each helminth species on the component community ordination score. Sites 1, 8 and 2 were largely influenced by the abundance of *P. tenerrima* (high dominance at these sites). Sites 4 and 6 were influenced by *C. brevivitellum*, and at site 3, *P. bulbocolli* was common. Furthermore, multivariate tests of the environmental variables, pH, flow rate and distance from sea on the CA ordination scores, revealed only pH to be a significant variable accounting for variability among helminth abundance ordination scores.

Contrary to the data on intestinal helminth infracommunities of *A. rostrata*, it appears local ecological conditions (e.g. pH- altering distribution of 'source' hosts) have a greater influence on richness and composition of intestinal helminth component

communities than do ontogenetic influences (host size-diet specificity).

Local vs. Regional Patterns

Barker *et al.* (1996) reported that a positive linear relationship existed between local helminth distribution (measured by maximum prevalence at any site) and regional helminth distribution (measured by the number of sample sites occupied by a species within a watershed and across Nova Scotia. They also concluded that the watershed be considered regional, in a functional sense, as the species pool of all available eel specialists approached a maximum (6 of 7) at the watershed level. A total of 8 species of metazoan parasites were reported (of a possible 12 species across Nova Scotia) within one watershed. The present study further emphasizes this relationship as 11 (of a possible 12) species were found within the same watershed as used by Barker *et al.* (1996). The 3 new species recovered were all generalists (2 autogenic, 1 allogenic), consistent with the idea that as host range expands there is an increase in the number of generalist species acquired (as the probability of encountering additional fish species increases) (Kennedy and Bush, 1994). The increase in species number was a product of sampling effort: one month (Barker *et al.*, 1996) as opposed to 2 years in the present study.

The 'core-satellite' model of Hanski (1982) was not supported by the present data. *Paraquimperia tenerrima* fits the definition of a core species, especially in June, but at site 6 (highest pH site), *C. brevivitellum* would be considered the core species and *P tenerrima* was sometimes rare. Several species that were regionally 'rare' (*C. brevi-vitellum, A. longa, P. bulbocolli, P. anguillae*) were at times locally abundant (at sites 5-

7). The core species of a population of eels at one site would be the satellite species of a population of eels at another site. Hartvigsen and Halvorsen (1993) reported the same discrepancy among helminth communities of trout, with regionally rare species being locally abundant. Hanski's (1982) model also predicts core species should be the first to invade a newly introduced host species. Elvers and juvenile eels (< 10 cm) could be considered 'introduced species', within the spatial scale of a watershed, and they are first infested by either *P. tenerrima* or *P. bulbocolli*. *Parquimperia tenerrima* could be considered as a core species, but not *P. bulbocolli*, which would be more of a satellite species. Perhaps Hanski's (1982) model, based on free-living theory, does not apply well to parasites due to the complexity of various 'intermixed' processes (e.g. transmission, abiotic factors, ontogenetic influences, etc.)

With respect to regional processes influencing local species richness, Kennedy (1990) questioned how closely linked were helminth component and infracommunities. Was the component community a sum of all infracommunities ? Alternatively, are infracommunities 'subsets' of both component and compound communities ? If the latter were true, under suitable conditions (component community diverse and transmission rates high), he predicted the infracommunity richness should be quite high. No evidence of such increases in infracommunity richness could be found among populations of *A. anguilla* in England (Kennedy, 1990; Kennedy and Guegan, 1996). However, some data to support the latter condition (infracommunities as 'subsets') were observed in the present study as illustrated in the highest mean species richness of both intestinal helminth infracommunity and total parasite assemblage/eel among those eels residing at the sites of highest pH (sites

of richest component communities). In addition, within the watershed, 3 sample sites (of high pH) had a total parasite assemblage richness (all months pooled) of 10 (of a possible 11 species). Kennedy and Guegan (1996) noted that variations in the helminth component community richness (CCR) was not reflected in variations in helminth infracommunity richness (ICR) of *A.anguilla*, and that a curvilinear model best fit the relationship of CCR and ICR. Such a curvilinear model suggests ICR became increasingly independent of CCR. These trends were not a result of proportional sampling, whereby ICR is always a fixed proportion of CCR (Cornell, 1984). Their results showed values of CCR to be much higher than that of ICR which approached an asymptote of 4 species, prompting their speculation of a fixed number of niches for helminths in the intestine of eels. In the present study, the helminth data on eels < 35 cm does support their findings, but larger eels (45+ cm) were found with 6 species of intestinal helminths. Plots of CCR and ICR for intestinal helminths of *A. rostrata* within a watershed (Figure 33a), were comparable to those for *A. anguilla* across Britain (Kennedy and Guegan, 1996). This implies that some type of 'limit' on the number of intestinal helminth species also exists for *A. rostrata*. Further studies are necessary to distinguish if this limit is a result of host size (available spaces to colonize) or interspecific interactions (or both). The patterns do support the findings of Kennedy and Guegan (1996) that the structure of helminth infracommunities is more influenced by 'bottom-up' (e.g. host factors) than 'top-down' (local environment) processes. However, the results of the present study also suggest both processes are not mutually exclusive.

On a larger spatial scale, Kennedy and Guegan (1994) concluded regional parasite

species richness (e.g. across Britain) was not a key determinant of local parasite species richness in freshwater fishes of Britain. In addition, a knowledge of regional species richness did not improve predictability of local species richness. Such studies, although they fail to establish a link between local and regional processes affecting parasite species richness, should not be misinterpreted as implying that local processes are unimportant. Regional species richness obviously sets a theoretical boundary for local species richness. Kennedy (1990) stated, in freshwater, where habitats are discontinuous, isolated and sometimes ephemeral, local factors affecting transmission should be more important than regional (phylogenetic) factors. Janovy *et al.* (1992) emphasized the importance of looking for the source of parasite assemblage structure within local environmental conditions *including* host related (ontogenetic) factors. Hartvigsen and Kennedy (1993), after examining helminth communities among brown trout in England, concluded local factors promoting distinctiveness have a greater influence on the composition and richness of fish helminth communities in lakes than do regional factors promoting similarity. Conversely, among free-living organisms, it has been traditionally accepted that the principle direction for control of species richness is from regional *to* local, such that keys to community structure are found in extrinsic biogeography, rather than in intrinsic local processes (Ricklefs, 1987; Cornell and Lawton, 1992).

4.5 Applicability as 'Bio-Tags'

There has been a common factor among all results in the present study (eel diet, mark-recapture, infracommunity richness and composition, component community

richness and composition) - an amazing consistency from 1995 through 1996. With such consistency comes predictability. The high proportion of specialists among the parasite communities of *A. rostrata* (as compared to *A.anguilla*) may account for the predictability of the parasite data (but it does not explain the consistency of patterns in eel biology). Consistency and predictability are 2 of several criteria necessary for a parasite to be a valid biological tag (bio-tag) (MacKenzie, 1987). In addition, there are several other favourable trends in the present data: (i) strong degree of site fidelity of the host helps promote and maintain heterogeneity of the parasites' distributions; (ii) preferred sites (site specificity) of some parasites, at pH > 5.5 = high abundance of *A.longa, C. brevivitellum, P. bulbocolli, P. anguillae* and at flow rates < 1.5 cm/s = high abundance of *P. anguillae* and *E. celestis*; (iii) size specificity of some parasites (*A.longa, E. celestis, P. anguillae, P. macrocephalus* - very abundant in large eels and (iv) annual downstream seaward migration of maturing silver eels.

In the present study, monthly peaks in plots of mean length coincide with monthly peaks in mean abundance of *A.longa* and *E. celestis*, indicating the downstream migration of maturing (silvering) eels from site 5 to site 1. While migrating, they carry parasites to downstream sites where they were previously uncommon. Interestingly, these parasites fail to establish at their 'new' locales and are absent the following spring. The higher infracommunity richness of silver eels at site 1 (compared with comparable sized yellow eels at site 1) and the grouping of silver eels with sites 3 and 5 (in cluster analysis), further emphasize that these silver eels previously inhabited some upstream site, where the component community was richer. Furthermore, the parasite assemblage composition of

the silver eels and the prevalence and abundance of each parasite species they harboured seem most typical of eels living in lacustrine habitats.

There are few studies of parasites as biological indicators of migration among populations of freshwater fishes (see discussion in Frimeth, 1987), but there are numerous studies documenting the success of parasites as biological indicators in populations of marine fishes (see reviews of Mackenzie, 1987; Lester, 1990; and collection by Arthur, 1995). In addition, many studies using parasites of marine fishes as valid predictors of pollution stress in an ecosystem are documented (Khan and Thulin, 1991; Barker *et al.*, 1994a; 1994b; Khan *et al.*, 1996). Conversely, there exists a paucity of literature using parasites of freshwater fishes as predictors of pollution stress in an ecosystem (Khan and Thulin, 1991 cite 3; the results of Cone *et al.*, 1993 and Marcogliese and Cone, 1996 are closely linked to the present study; see upcoming review in Marcogliese and Cone, 1997b). There exists quite a paradox related to studies using parasites of marine fishes as bio-tags (Holmes, 1990b). The helminth communities of marine fishes are dominated by generalists - yet they show predictability. A high composition of generalists among a parasite community implies a strong degree of stochastisity with respect to structuring processes, yet these communities of marine parasites appear 'structured'. The lack of studies of this type on freshwater helminths may reflect their 'stochastic' nature, or it may reflect a different emphasis of study. The parasite fauna of *A. rostrata*, dominated by specialists, exhibiting annual consistency should be suitable as bio-tags, and would be a valuable tool in fishery management studies as an indicator of localized eel dispersal within a watershed and as indicators of pH gradients locally (within a drainage system) and

regionally (across the province).

4.6 Benthic Stream Macroinvertebrate Assemblages

Remarkable parallels existed between patterns of richness and diversity among benthic macroinvertebrate assemblages and intestinal helminth component communities of *A. rostrata* in the present study. The sites of lowest helminth component community richness (sites 8, 1 and 2) were also the sites of lowest macroinvertebrate richness (measured by number of families). (Bournaud *et al.* (1996) noted that differences at the familiy level were sufficient in comparisons of habitat quality using benthic stream macroinvertebrates.) The sites of highest helminth component diversity and evenness (sites 3-7), were also the sites of highest macroinvertebrate diversity and evenness. The increased richness observed at sites of high pH was by accumulation of macroinvertebrate taxa (see Appendix C) that are reportedly sensitive to pH (Hynes, 1970; Peterson *et al.*, 1985; Sutcliffe and Hildrew, 1989; Muniz, 1991; Schindler *et al.*, 1991). Differences in the abundance of intermediate 'source' hosts also parallel differences in abundances of their respective helminth species. The sphaerid clams were very abundant at sites 5 and 6, the sites of highest abundance of *C. brevivitellum.* Similarly, the high abundance of Trichoptera (Hydropsychidae and Polycentropodidae) and Chrionomidae at sites 8, 1 and 2 presumably reflected the high abundance of *P. tenerrima* at these same sites, thus providing more evidence of favour of these larval insects as suitable 'source' hosts. The linkage between abundance of helminth species and abundance of 'source' hosts was clearly demonstrated in the ordination results: (i) using helminth data, sites 4 and 6 had

similar ordination scores based on abundance of *C. brevivitellum*; using macroinvertebrate abundance, sites 4 and 6 had similar ordination scores based on abundance of sphaerid clams (Bivalvia) and other acid-sensitive species; (ii) sites 8, 1 and 2 had similar ordination scores based on abundance of *P. tenerrima* using helminth data, and they had similar ordination scores based on abundance of Trichoptera (Hydropsychidae and Polycentropodidae) and Diptera (Chironomidae); (iii) site 3 had a high abundance of *P. bulbocolli* and *B. claviceps* and its ordination score using macroinvertebrate taxa was largely influenced by an abundance of amphipods. These results may imply one (or several) species of amphipod can serve as 'source' host for *B. claviceps*. Amin (1978) reported several species of crustacea to be hosts of various cestodes.

The ordination distance between sites using macroinvertebrate data was smaller than the distances produced using helminth abundance data, a factor of the increased number of common taxa among the sample sites, and is more evidence in favour of using parasites as indicators of ecosystem stress. As with the helminth component community data, pH was the only significant factor accounting for the variation among ordination scores of the macroinvertebrate data. The apparent reduction in macroinvertebrate diversity at sites of low pH (< 5.4) is consistent with results of other studies (Hynes, 1970; Peterson *et al.*, 1985; Sutcliffe and Hildrew, 1989; Muniz, 1991; Schindler *et al.*, 1991).

The observed feeding specificity among sites appears to be a consequence of differences in local macroinvertebrate assemblages, consistent with the theory of opportunistic foraging behaviour in eels. For example, the highest abundance of amphipods was at site 3, and it was this site that had the highest percentage of eels

consuming amphipods. The macroinvertebrate data presented are limited as they are merely a 'snapshot' of a dynamic assemblage of animals and are misrepresentative of seasonal changes in composition. Perhaps if these samples were taken in May, diversity indices would indicate high dominance of Ephemeroptera at all sites, corresponding to a seasonal 'bloom' (as evidenced by eel stomach contents and personal observation in the field). However, calculation of ecological indices (H', N2, J', λ) using macroinvertebrate abundance data (at taxon of Order) from DFO during 1988-1995 at sites 8, 4 and 6, resulted in values within the range reported for those same sites in the present study. Another interesting observation was that these macroinvertebrate samples were collected approximately 2 weeks after the first spate of 1996, yet there appeared to be no indication of increased richness downstream associated with displacement by the flood as might be expected (Hynes, 1970). This may be indicative of the resilience of these assemblages. If such is true, their regularity within the catchment may be a factor contributing to the consistency of patterns observed among the distribution of helminths from 1995 to 1996.

Based on congruence of patterns between: (i) distribution of intestinal helminths and macroinvertebrate source hosts and (ii) richness and diversity of helminth component communities and macroinvertebrate assemblages, it would seem the limited macroinvertebrate data set was actually sufficient. Furthermore, the speculations of Cone *et al.* (1993) and Conneely and Mcarthy (1986) that patterns among helminths of eels are a result of patterns among local macroinvertebrate assemblages are supported in the present study. In the present study, It would appear pH is affecting the transmission success of the parasites by affecting the distribution and abundance of macroinvertebrate

source hosts. A variation of the 'numerically dominant host' concept of Leong and Holmes (1981) seems appropriate: rather than the numerically dominant *definitive* host present in an aquatic system, it seems the numerically dominant *intermediate* host (e.g. macro-invertebrates) influences helminth component communites of *A. rostrata*.

4.7 Processes Structuring Parasite Communities in *Anguilla rostrata*

The present data provide evidence that helminth communities of *A. rostrata* are structured, characterized by annual consistency and congruence of patterns. The high dominance by specialist parasites implied a phylogenetic component was associated with helminth community structure. This was one of the most distinctive differences in the composition of helminth infra- and component communities between the sister species *A. rostrata* and *A. anguilla*. At the infracommunity level, host size (specificity of diet), an ontogenetic factor, appeared to be most influential in determining helminth species richness in *A. rostrata*. Another difference between patterns in helminth communities between *A. rostrata* and *A. anguilla* could have been attributed to the increased proportion of larger hosts (45+ cm) in the present study. Further obscuring any noticeable effects of phylogenetic influence on helminth infracommunity richness in *A. anguilla* might be the increase in fish species (thus increase in potential to acquire generalist species) in the United Kingdom compared with Nova Scotia.

Ontogenetic influences appear to less important than local ecology (specifically, pH) in determining richness and composition of the helminth component communities of

A. rostrata in the present study. One goal of parasite community ecology is to search for how the structure of intestinal parasites (that are ingested) is achieved. The influence of local conditions affecting food webs, thereby affecting distributions of source hosts, cannot be ignored. Ironically, the literature emphasizes the 'final result' (processes affecting infracommunity structure in the definitive host), and has often overlooked the 'structure' of macroinvertebrate assemblages, which houses the pool of transmission stages for these parasites. It may be that diet is the prime determinant of intestinal community structure. If one reviews all the hypotheses concerning intestinal helminth structure, it would seem each hypothesis can *ultimately* be linked to diet. As parasitologists had once turned to free-living ecology to attempt to explain patterns in parasite communities, perhaps it is time to once again turn to free-living ecology on a different scale. Maybe it is time to study the community structure of free-living macroinvertebrates which are 'source' hosts. There we may find the answer to the proximate processes that influence intestinal helminth community structure in fishes.

Both influential processes (ontogenetic and ecological) are not mutually exclusive, but it would appear the relative magnitude of their influence differs with scale (e.g. infra- or component community). It may be impossible to seek a universal hypothesis to explain how parasite communities in freshwater fishes (and/or other vertebrate groups) are structured, nor was that the goal of this study. However, I feel the present data on helminth communities in *A. rostrata* shed a new perspective on earlier studies of parasites in freshwater fishes and the respective roles of phylogeny and ecology in determining helminth community structure. Furthermore, this work complements the volumes of work

on helminths of *A. anguilla*.

To make an analogy, in *A. rostrata*, regional, evolutionary (ultimate influence) factors determine a 'menu' - an eel could possibly have parasite A, B, C, ..., etc., these species can successfully colonize any eel of any given age. Local ecology, environmental conditions (proximate influence) factors is the 'currency' that determines what (and how much) gets selected from that menu - the composition of the helminth community and relative abundance of each species. And, it would appear that the helminth communities of *A. rostrata* living at sites of high pH in the present study were 'richer' than those reported for *A. anguilla*.

4.8 Future Studies

Current studies (present study included) on parasites of *A. rostrata* only form a baseline from which to diverge. There is more research that can and should be done. It is worthy to note that the watershed used in this study is somewhat artificial, in that its pH has been artificially raised, thus is significantly greater than nearby catchments. I prefer to consider the system as 'experimental' - it was applicable for the examination of patterns in helminth communities on a local scale, within pH gradients common to a regional scale (province). The DFO 'habitat deacidification program' terminated this past year (1997). It would be very interesting to see if richness and diversity of the helminth component communities in eels decrease over the next few years (as pH gradually declines), ultimately resembling that of sites 8, 1 and 2. Second, the issue of host size needs further assessment, perhaps a comparative study of only eels 45+ cm from a variety of habitats. Third,

experimental evidence is necessary to provide further insight on the role of interspecific interaction as a possible structuring process among intestinal helminth infracommunities of eels. Fourth, the macroinvertebrate assemblages should be re-examined, more specifically, for the distribution of *larval* helminths among the source hosts, as a means of quantifying the importance of food web interaction on successful transmission. Fifth, the helminth communities in eels from insular Newfoundland should be examined. The watersheds are of generally high pH (> 5.5), but they lack several fish species common in Nova Scotia. Presumably, less generalists would be observed among the helminth community - how would this affect predictability ? Sixth, conduct a survey of helminth parasites in eels across Atlantic Canada, examining the relationship of component community richness on infracommunity richness as was done for the British Isles. Would the higher percentage of specialists in *A. rostrata* affect previously described patterns ? Seventh, examine helminths of eels living in estuaries - again, examine patterns between CCR and ICR. Finally, for all advocates of non-anguillid fishes, extend these community analyses into other fish taxa, especially a comparison between indigenous and introduced species.

5. SUMMARY

1. Populations of *Anguilla rostrata* in the Timber Lake watershed were sedentary with restricted home ranges. There was evidence of upstream migration by elvers and juvenile eels (in the first and second years in freshwater) and downstream migration of sexually maturing 'silver' eels. During their third year in freshwater and extending to over 15 years, eels appeared to be localized residents at each of the sample sites and it is during this period that they acquire metazoan parasites. Eels were opportunistic foragers, but there was evidence of diet specificity (monophagy) associated with eel size. Several aspects of eel biology (size, diet, home range, migration) were shown to influence parasite fauna.

2. The species richness and parasite population of the intestinal helminth infracommunity and total parasite assemblage per eel increased with eel length, likely a consequence of physical (increase in available space to colonize) and biotic (diet selectivity - piscivory in large eels) influences. Most eels (~85%) had an intestinal helminth infracommunity species richness of only 1 or 2 species. For eels less than 35 cm, this richness did not exceed 4 species, but in large eels (45+ cm), this richness could be 5 or 6 species. Eel specialists dominated the majority of intestinal infracommunities.The evidence for interspecific interaction among intestinal helminths was equivocal; all observed patterns of parasite species-pair combinations could be explained by dietary specificity.

3. Several parasites (*Azygia longa, Proteocephalus macrocephalus, Ergasilus celestis* and *Pseudodactylogyrus anguillae*) were 'size-selective', being most common in larger eels. The distribution of four species (*A. longa, Crepidostomum brevivitellum,*

Pomphorhynchus bulbocolli, and *P. anguillae*) was related to pH; they were only found at sites of pH > 5.5. The abundance of both gill parasites (*E. celestis* and *P. anguillae)* was negatively correlated with stream flow, likely a consequence of difficulty of transmission. The period of peak recruitment of the 8 'common' metazoan parasites recovered was during the period of highest water temperatures, and presumably, a time of high eel abundance.

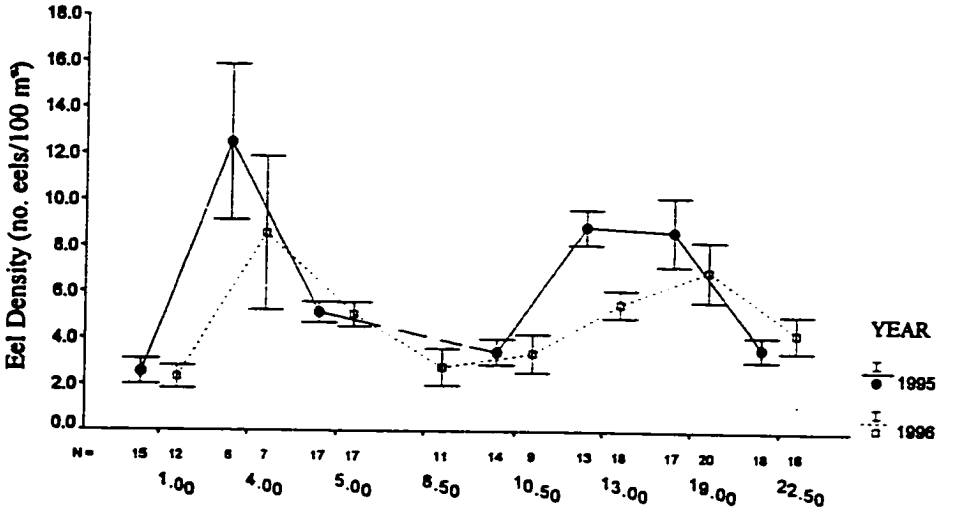
4. The intestinal helminth component community was influenced by pH gradients within the watershed. Heterogeneity of these component communities was maintained by localized eel residency. At the sites of low pH (4.2-5.3), helminth component communities were characterized by low species richness, low diversity and high dominance. Conversely, at the sites of high pH (5.5-6.8), helminth component communities were characterized by high species richness, high diversity and low dominance. Patterns among helminth component communities parallelled those of benthic stream macroinvertebrate assemblages sampled from the same sites. Ordination analyses illustrated the link between parasite abundance and macroinvertebrate 'source' host abundance as influenced by pH. As with eel infracommunities, the majority of component communities were also dominated by specialists.

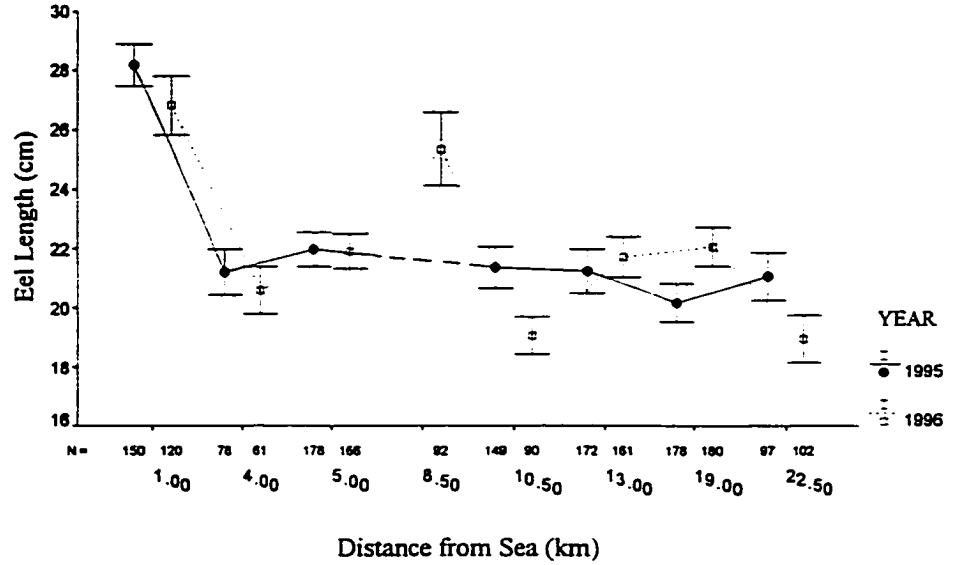
5. For eels less than 35 cm, the infracommunity richness (ICR) became increasingly independent of component community richness (CCR). High values of CCR did not result in an increase in ICR - a 'saturation' or 'ceiling' effect was observed at the infra-community level. There was little evidence in favour of proportional sampling or supply side ecology (i.e., ICR directly dependent on CCR). The total richness of eel parasites at

the watershed scale was 11 species (of a possible 12 across Nova Scotia). This complimented previous work which concluded the watershed be considered regional (for eel parasites) in a functional sense as it contains the species pool of all available eel specialists.

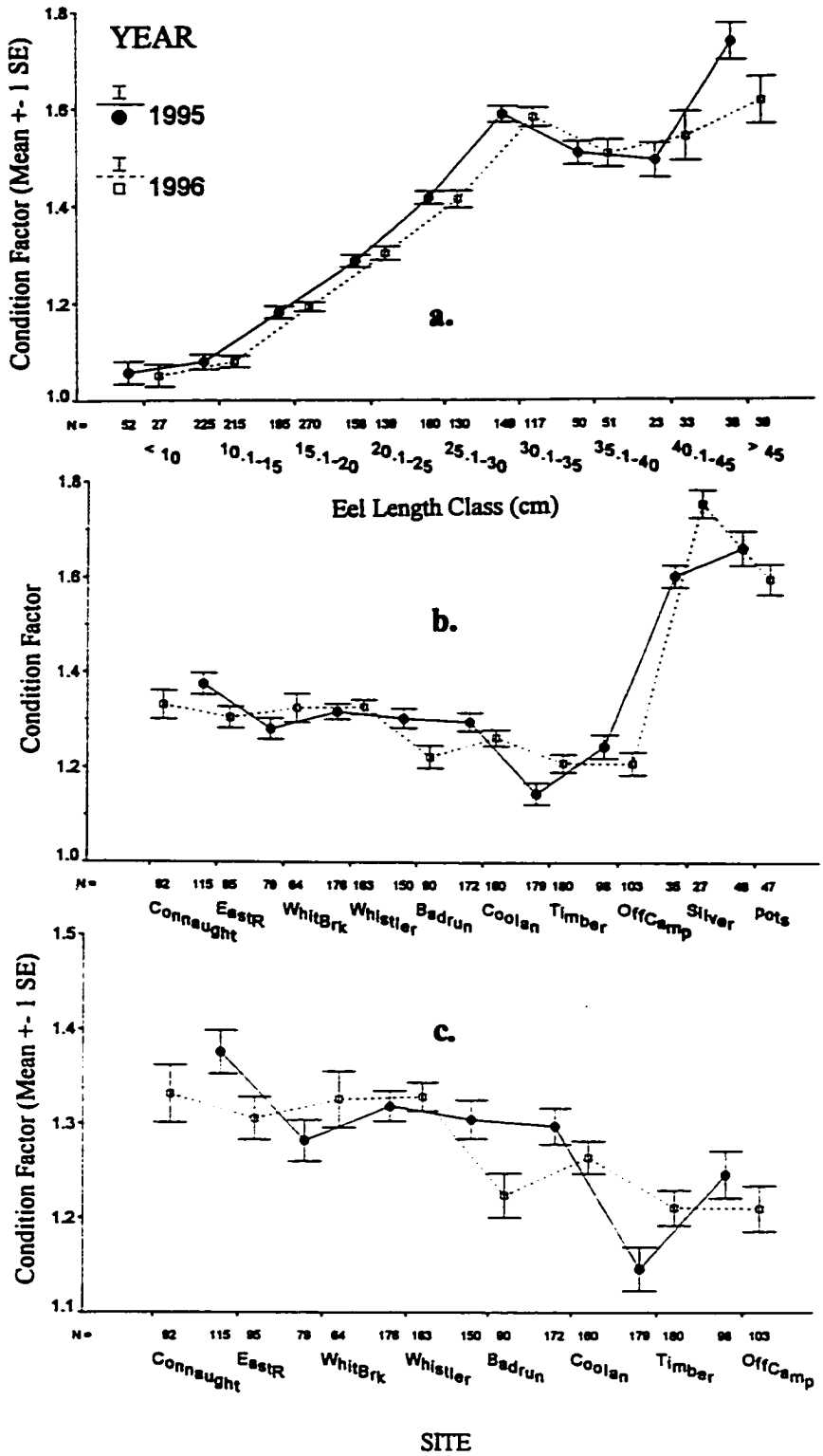
6. The downstream migration (from July-October) of sexually maturing silver eels could be plotted using changes in abundance of 2 'size-selective' eel parasites (*A. longa* and *E. celestis)*. These species (and others) were carried downstream (by seaward migrating maturing eels) to locales where they were previously absent or uncommon among populations of yellow eels. These "new immigrants" failed to colonize at their new sites the subsequent season. It was suggested that parasites whose prevalence and abundance was highly influenced by host-related (size) or abiotic factors (e.g. pH or flow rate sensitive) could be suitable as biological tags - indicators of eel riverine dispersal and / or habitat pH level.

7. The annual consistency of patterns and predictability of the infra- and component communities was attributed to the high proportion of specialists dominating these communities. It was concluded that ontogenetic influences (host biology) were more evident at the infracommunity level, but ecological influences (pH affecting macroinvertebrate assemblages) were more evident at the component community level. However, both processes were not mutually exclusive and it was suggested phylogenetic (ultimate) influences were responsible for determining potential parasite richness (e.g. an eel could have 'X' species of parasites); but, local environmental (proximate) influences were responsible for determining parasite community composition and abundance.

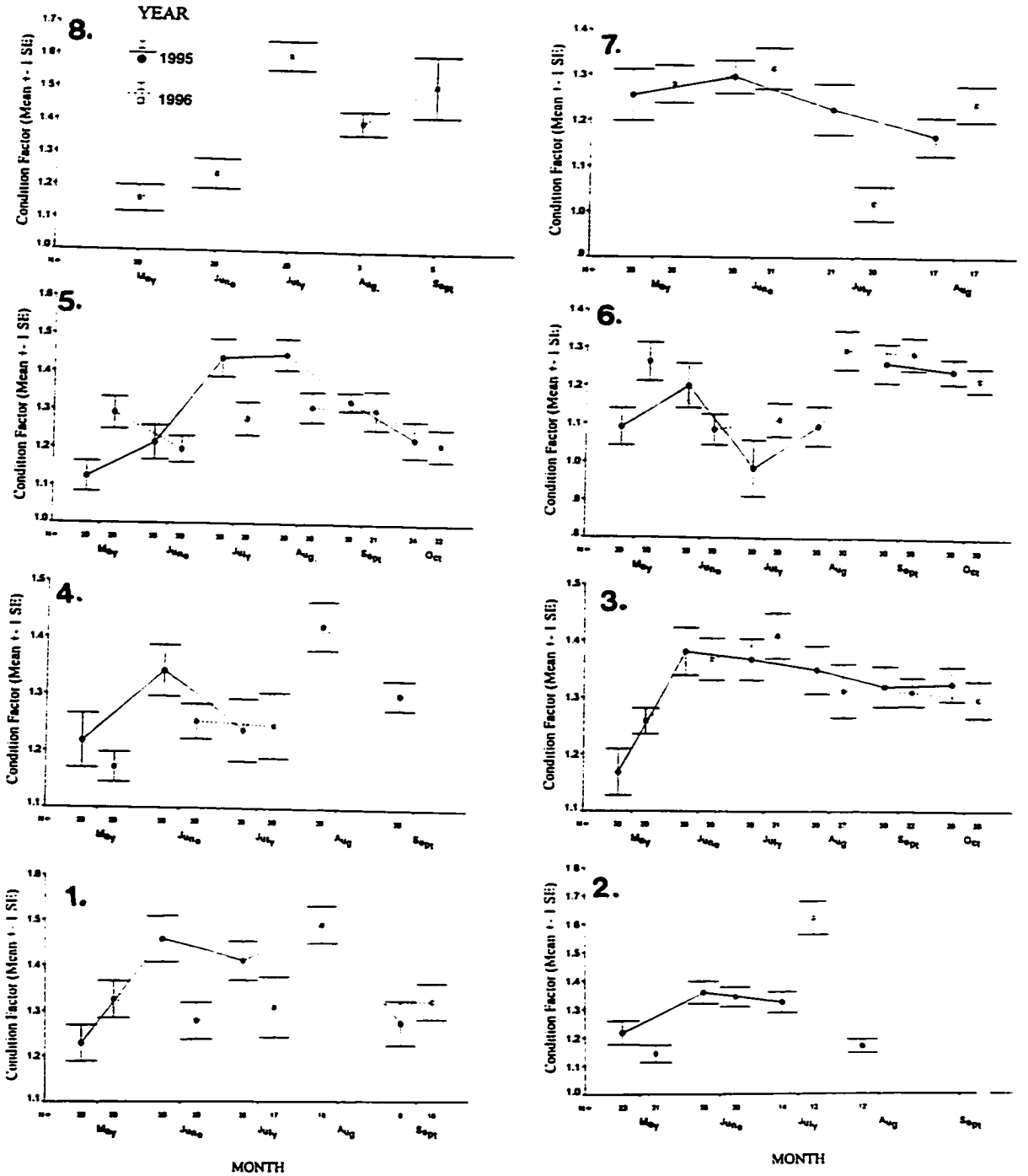




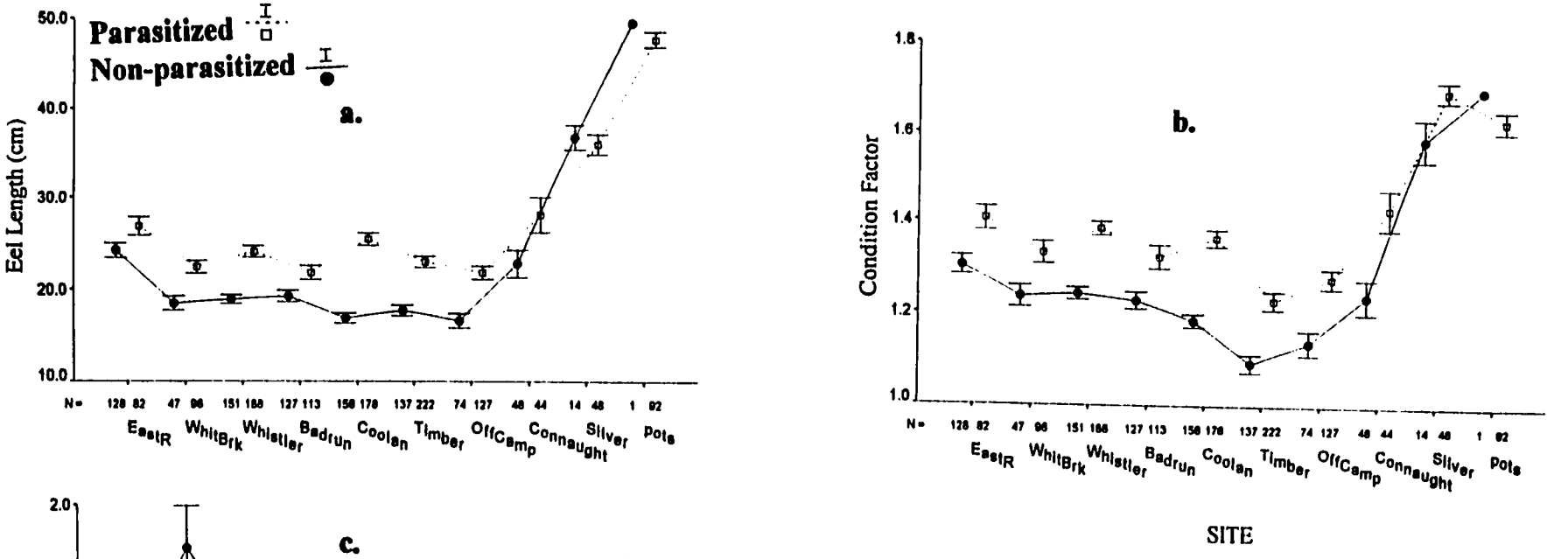
Appendix A1. Annual mean (±s.e.): (a.) eel density estimates and (b.) eel length (cm) per distance from sea (km).



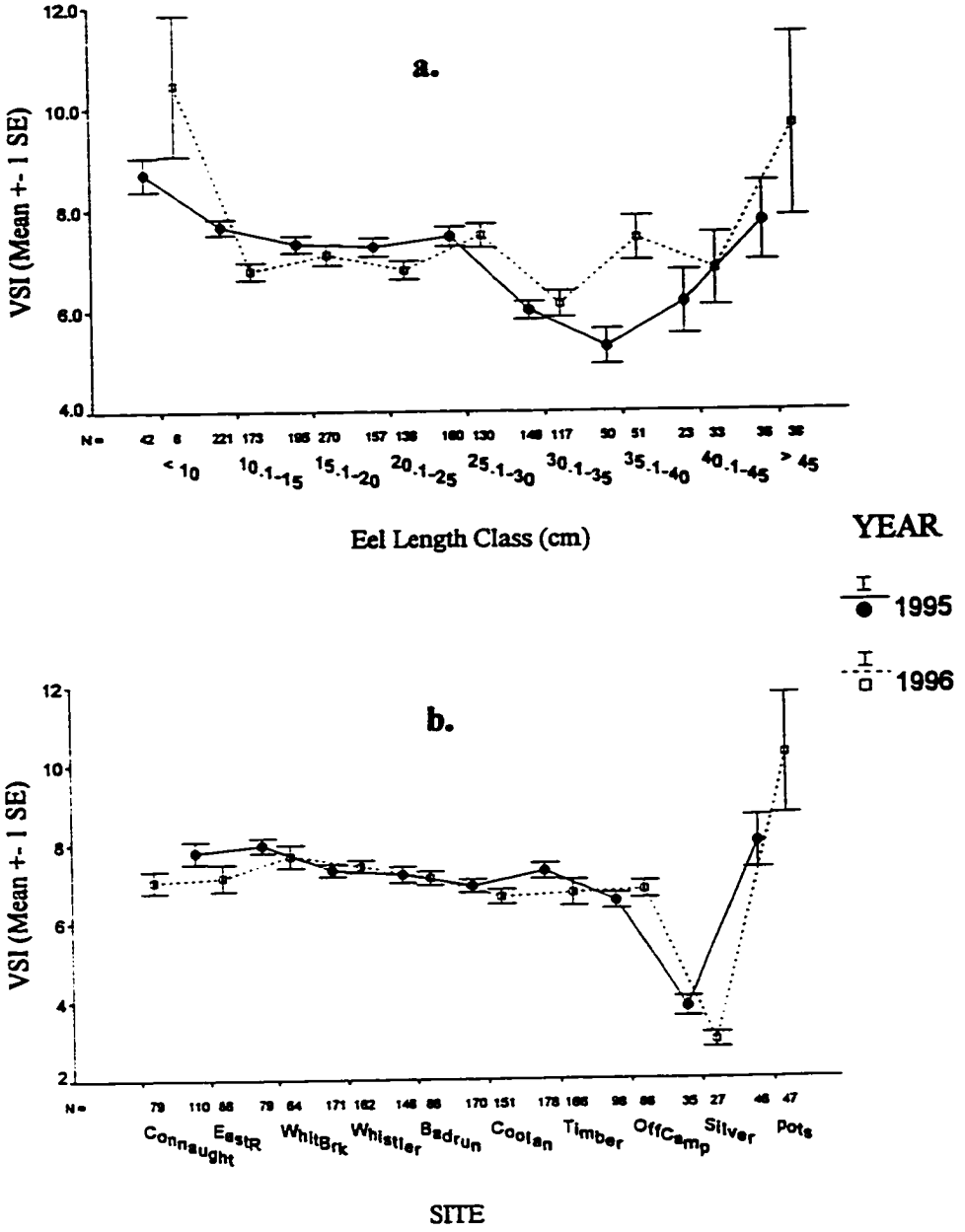
Appendix A2. Annual mean (±s.e.) condition factor [(weight/length^3)x1000] of : (a.) each eel length class; (b.) each sample site, including silver and potted eels; (c.) electrofished eels only during 1995 and 1996.



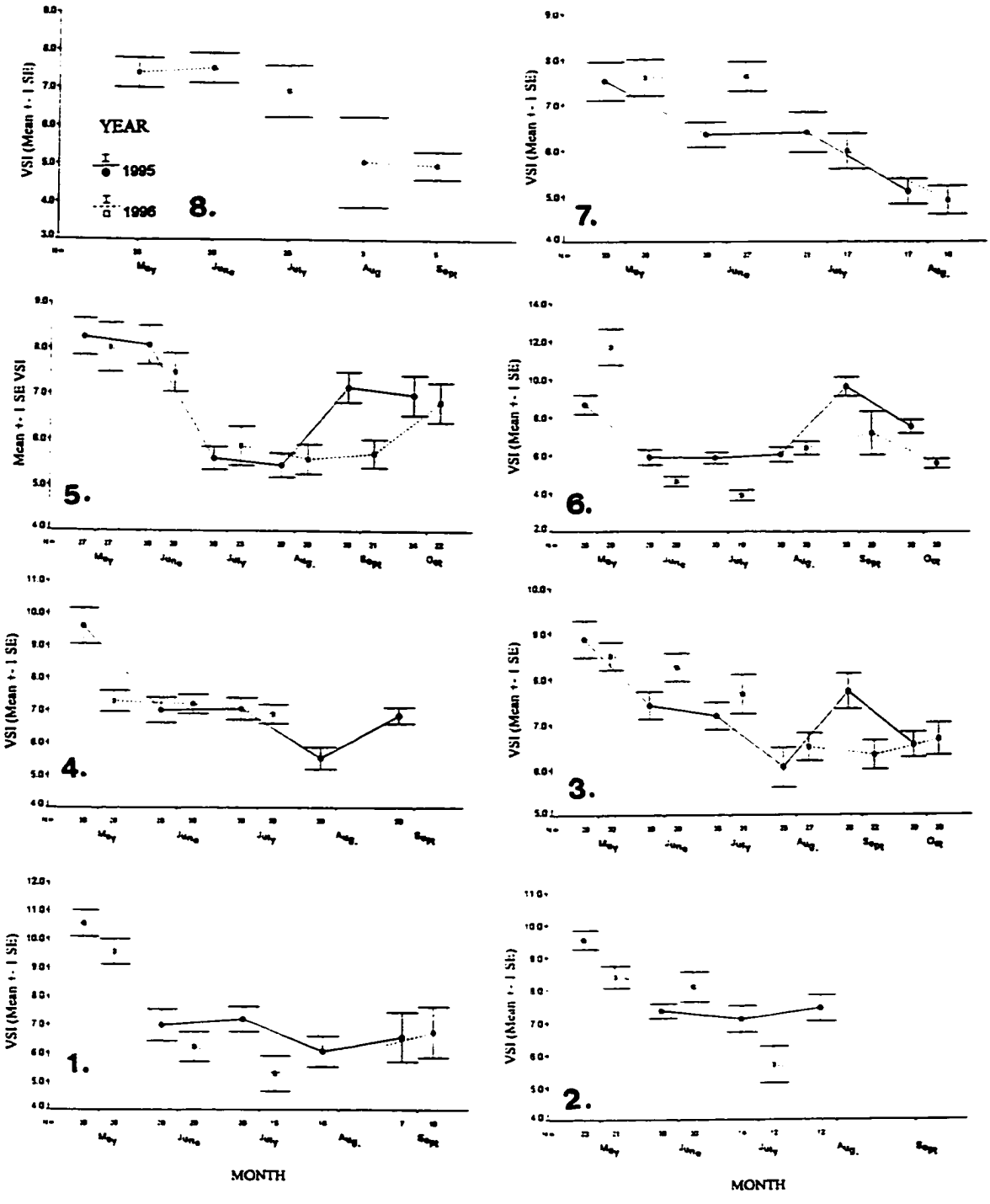
Appendix A3. Monthly mean (±s.e.) condition factor [(weight/length^3)x1000] at each sample site during 1995 and 1996.



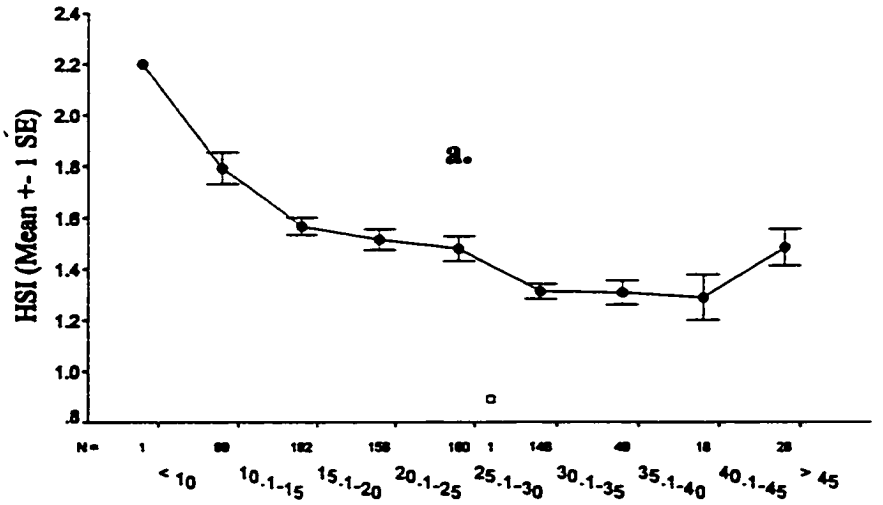
Appendix A4. Total mean (±s.e.): (a.) length; (b.) condition factor and (c.) hepatosomatic index (HSI) between parasitized and non-parasitized eels during 1995 and 1996.

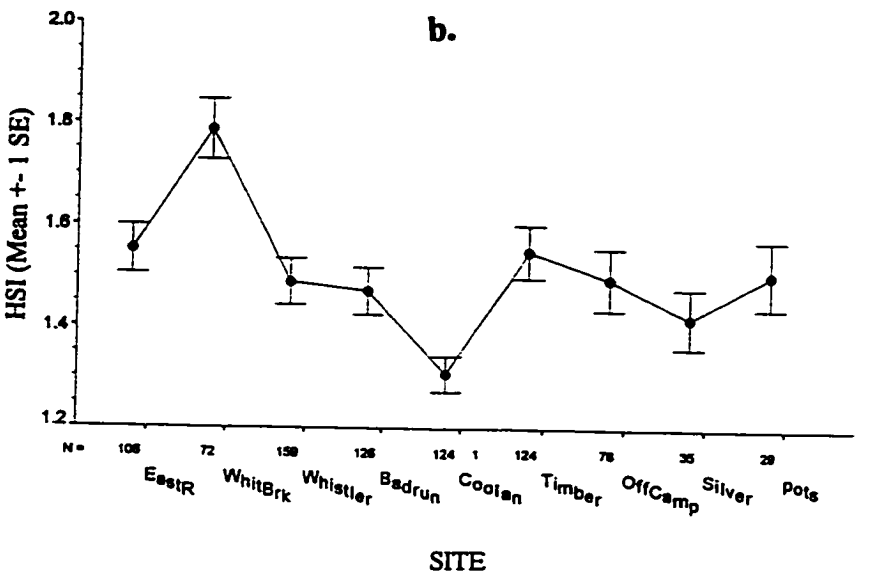


Appendix A5. Annual mean (±s.e.) visceralsomatic index [VSI = (stomach weight/ body weight) x100] of : (a.) each eel length class; (b.) each sample site, including silver and potted eels during 1995 and 1996.

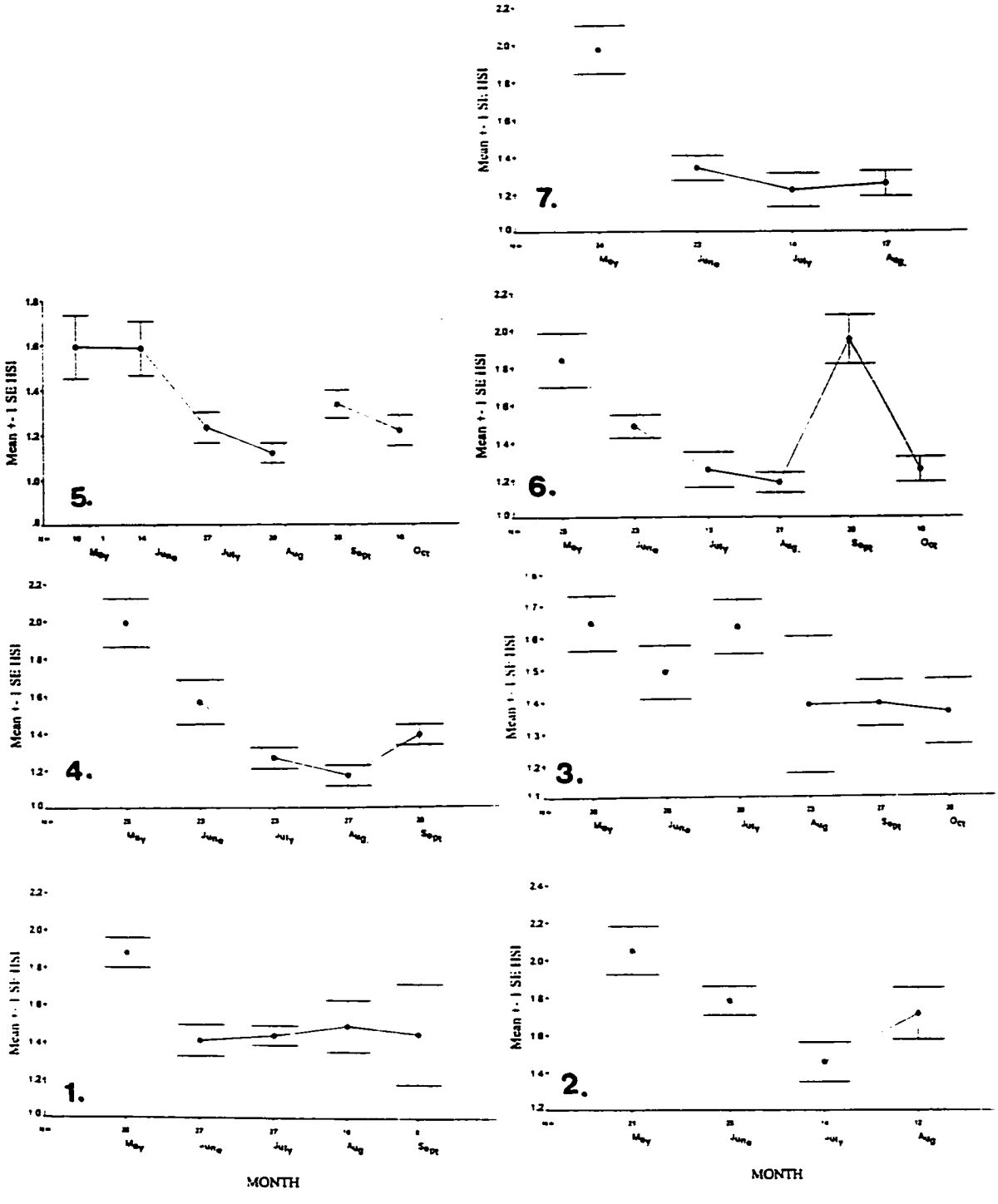


Appendix A5c. Monthly mean (± s.e.) visceralsomatic index [VSI = (stomach weight/ body weight) x100] at each sample site during 1995 and 1996.

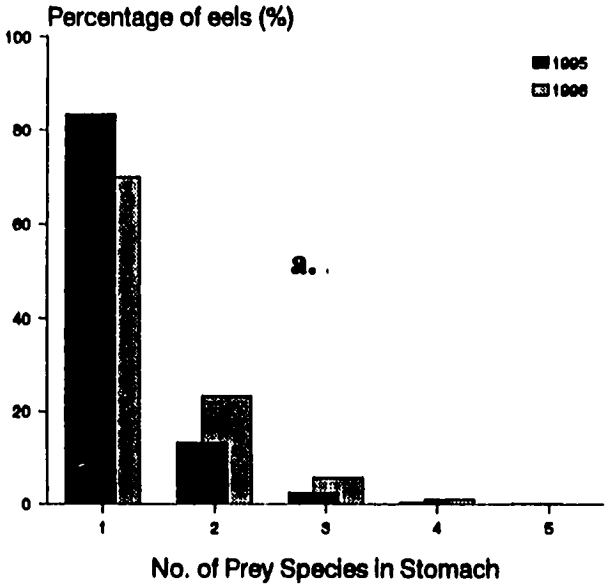


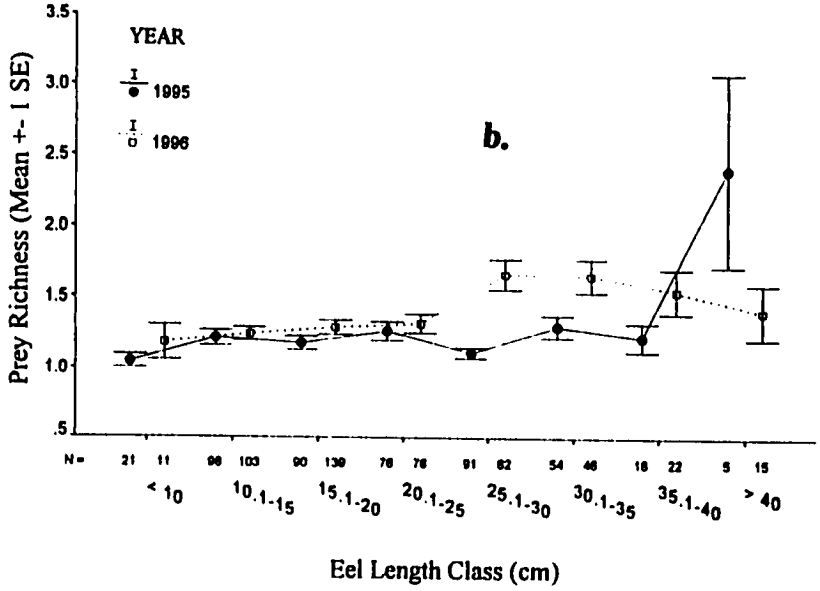


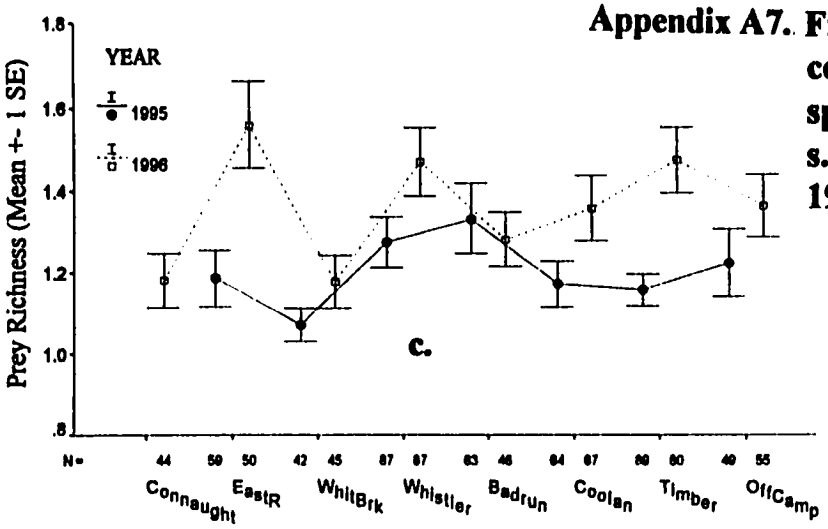
Appendix A6. Annual mean (±s.e.) hepatosomatic index [HSI = (liver weight/ body weight) x100] of : (a.) each eel length class; (b.) each sample site, including silver and potted eels during 1995.



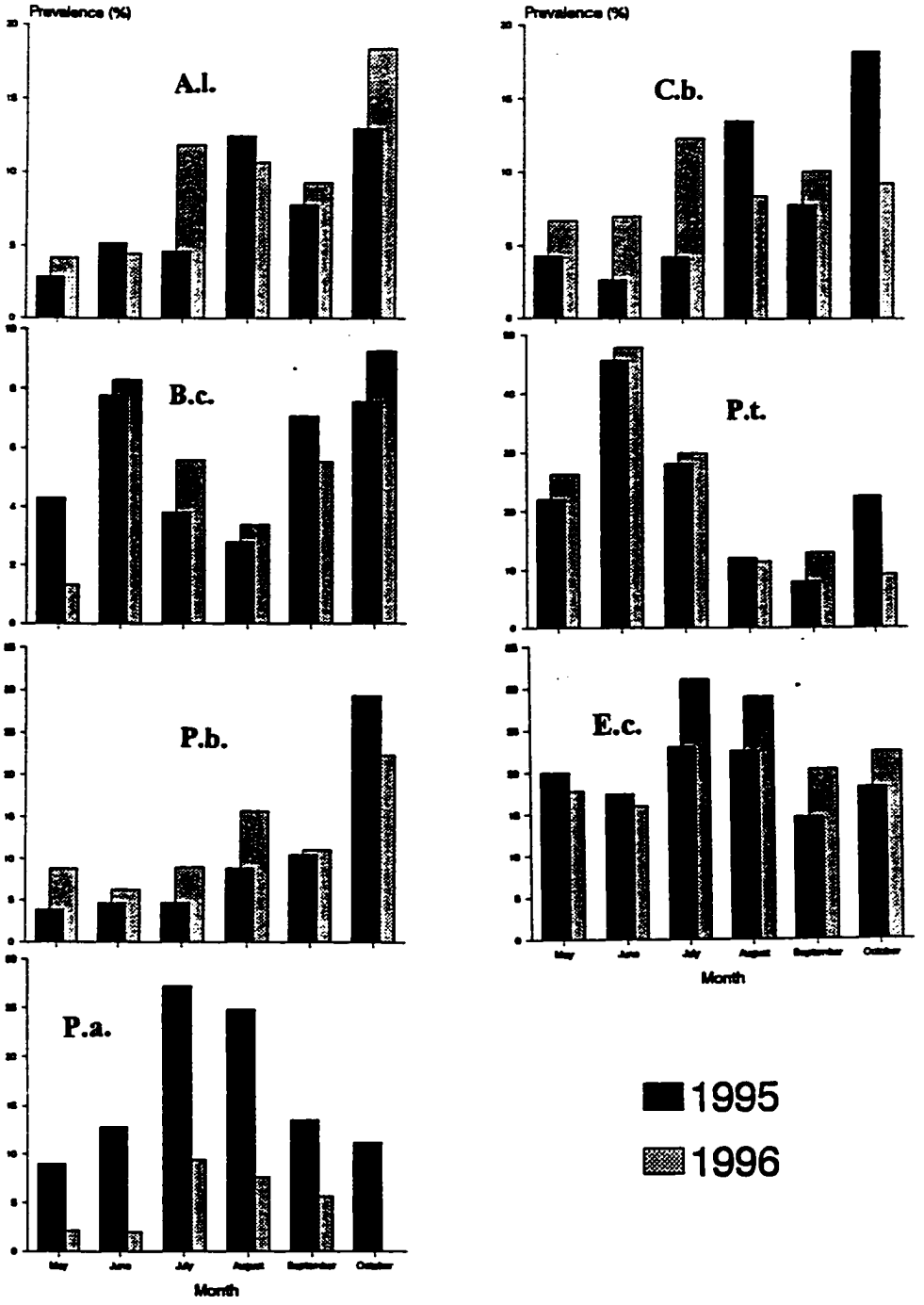
Appendix A6c. Monthly mean (± s.e.) hepatosomatic index [HSI = (liver weight/ body weight) x100] at each sample site during 1995.





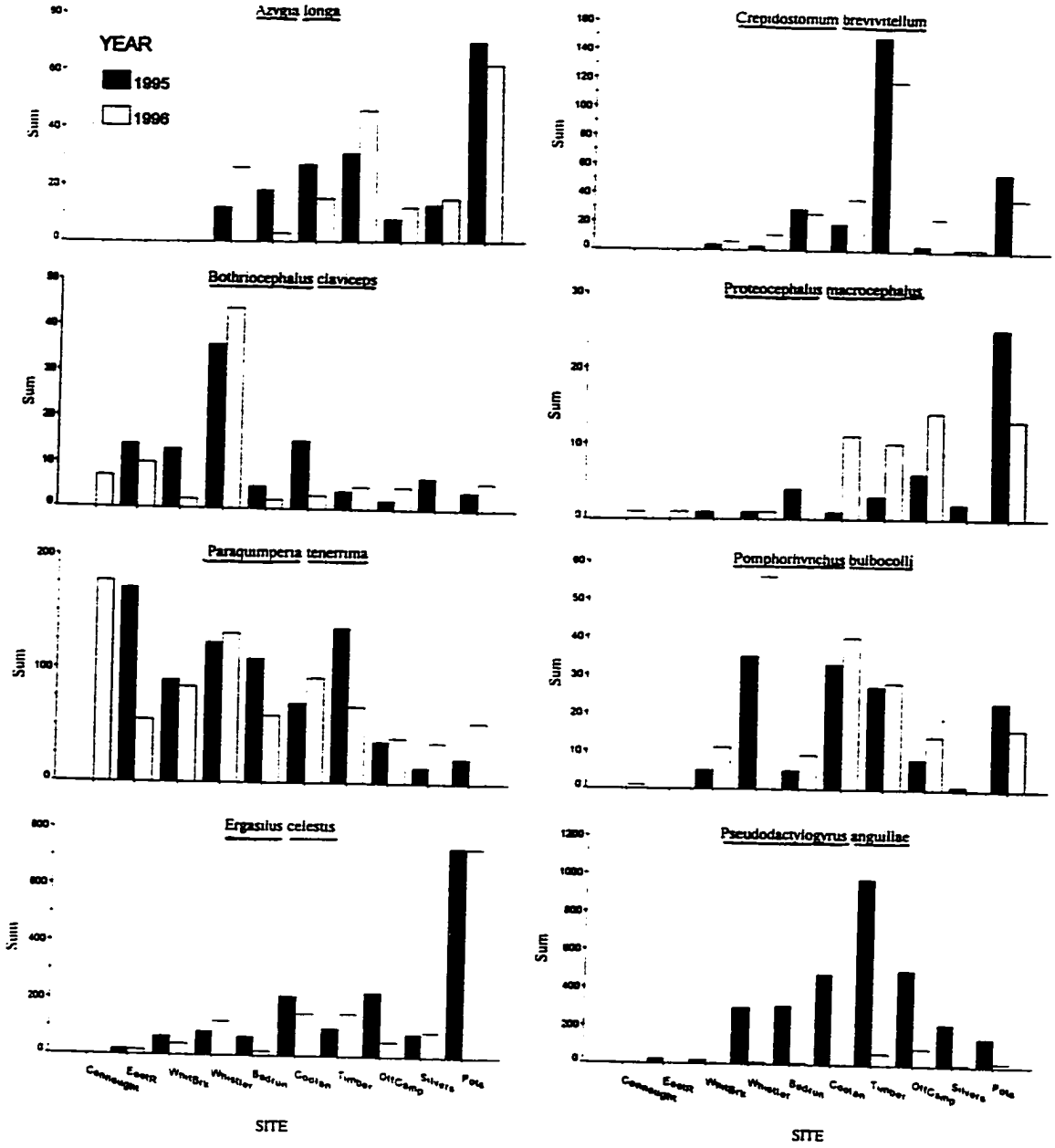


Appendix A7. Frequency distribution (a.) of the numbers of different prey species consumed by each eel; (b.) annual mean (± s.e.) number of prey species consumed by each eel length class and (c.) annual mean (± s.e.) Number of prey species consumed at each sample site during 1995 and 1996.



Appendix B1. Total monthly prevalence (%) during 1995 and 1996 of 7 common metazoan parasites in the Timber Lake Watershed.

(C.b.= *Crepisdostomum brevivitellum*; A.l. = *Azygia longa*; B.c. *Bothriocephalus claviceps*; P.m. = *Proteocephalus macrocephalus*; P.t. = *Paraquimperia tenerrima*; P.b. = *Pomphorhynchus bulbocolli*; E.c. = *Ergasilus celestis;* P.a. = *Pseudodactylogyrus anguillae)*



Appendix B2. Total numbers (sum) of the 8 common metazoan parasites per sample site during 1995 and 1996.

	SITE NUMBER							
Macroinvertebrate Taxon	1.	2.	3.	4.	5.	6.	7.	8.
O. EPHEMEROPTERA (Total)	19	33	50	87	52	140	13	0
F. Baetidae	16	31	50	67	47	110	13	0
F. Heptageniidae	3	2	0	20	5	30	0	0
O. ODONATA (Total)	9	107	24	52	35	164	17	12
F. Coenoagrionidae	2	5	3	17	9	12	4	6
F. Agrionidae	0	10	1	16	8	12	1	0
F. Gomphidae	7	5	8	6	8	115	7	0
F. Aeshnidae	0	87	12	12	10	19	5	6
F. Libellulidae	0	0	0	0	0	6	0	0
O. PLECOPTERA (Total)	8	9	3	7	0	7	4	5
F. Perlidae	2	0	0	5	0	5	0	0
F. Leuctridae	6	9	3	2	0	2	4	5
O. HEMIPTERA (Total)	0	0	1	0	0	12	6	0
F. Corixidae	0	0	1	0	0	10	4	0
F. Hydrometridae	0	0	0	0	0	2	2	0
O. TRICHOPTERA (Total)	94	325	139	290	161	231	352	330
F. Hydropsychidae	7	232	18	20	42	36	220	100
F. Brachycentridae	13	19	25	75	12	40	26	17
F. Polycentropodidae	10	65	10	40	61	35	73	160
F. Lepidostomatidae	17	0	26	30	3	10	3	45
F. Helicopsychidae	15	0	15	50	3	50	0	0
F. Hyrdroptilidae	0	0	0	35	10	20	0	0
F. Leptoceridae	32	9	45	40	30	40	30	8

Appendix C. Total abundances of each macroinvertebrate taxon based on 3, 1m² quadrants at each sample site. **(Continued next page)**

	SITE NUMBER							
Macroinvertebrate Taxon	**1.**	**2.**	**3.**	**4.**	**5.**	**6.**	**7.**	**8.**
O. COLEOPTERA (Tot.)	33	116	76	155	59	119	128	13
F. Gyrinidae	3	8	4	11	4	8	25	4
F. Psephenidae	24	0	5	10	25	44	20	0
F. Dryopidae	6	108	67	134	20	65	83	9
O. DIPTERA (Total)	160	260	109	74	62	178	311	200
F. Chironomidae	156	240	105	68	60	160	300	200
F. Tipulidae	4	16	4	4	0	10	8	0
F. Rhagionidae	0	3	0	1	0	5	1	0
F. Tabanidae	0	0	0	1	2	3	2	0
O. AMPHIPODA	2	3	130	0	14	12	45	2
C. TURBELLARIA	2	0	3	39	77	60	3	7
P. ANNELIDA (Total)	13	16	33	16	26	118	89	13
C. Oligochaeta	13	16	31	15	20	115	85	11
C. Hirudinea	0	0	2	1	6	3	4	2
P. MOLLUSCA (Total)	0	14	21	132	255	285	147	0
C. Bivalvia	0	14	21	122	220	180	140	0
C. Gastropoda	0	0	0	10	35	105	7	0

Appendix C (cont'd). Total abundances of each macroinvertebrate taxon based on 3, 1m² quadrants at each sample site.

Species	First Intermediate Host	Second Intermediate Host
Pseudodactylogyrus anguillae*	None	None
***Crepidostomum brevivitellum*‡**	Sphaeridae (clams)	*Ephemera,Hexagenia*(mayflies)
***Azygia longa*++**	Amnicolidae (snails)	Optional piscine transport
***Bothriocephalus claviceps*‡**	Copepoda	Optional Crustacea ? Fish ?
***Proteocephalus macrocephalus*‡**	Copepoda	Optional piscine transport
***Paraquimperia tenerrima*‡**	Chironomidae? Piscine ?	?
***Eustrongylides* sp.+** (accidental, matures in birds)	Oligochaeta	Piscine (*Fundulus,Catostomus)*
***Pomphorhynchus bulbocolli*‡**	Gammaridae (amphipods)	Optional piscine
***Neoechinorhynchus rutili*‡**	Gammaridae (amphipods)	Optional piscine
***Echinorhynchus salmonis*‡**	Gammaridae (amphipods)	Optional piscine
Ergasilus celestis*	None	None

Appendix D. Life cycles of the metazoan parasites collected from eels throughout the Timber Lake watershed. For further description and seasonality patterns refer to section 4.3.

Location within host: ‡ = intestine; ++ = stomach; * = gills; + = visceral mesentary

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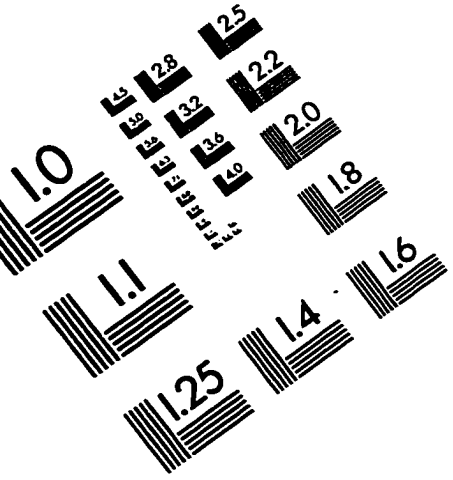
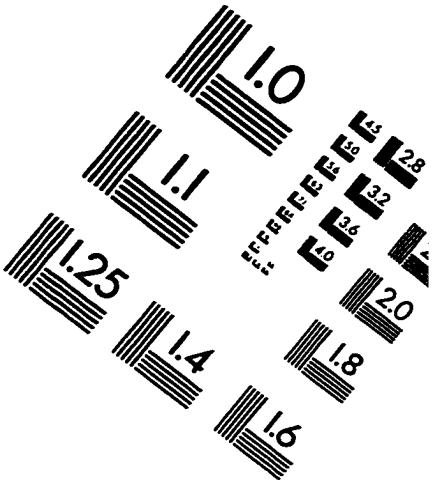
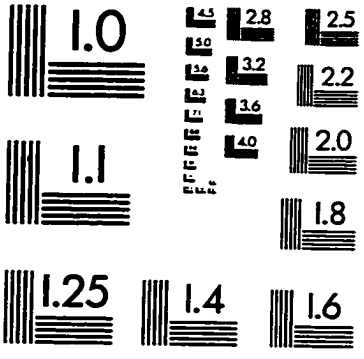
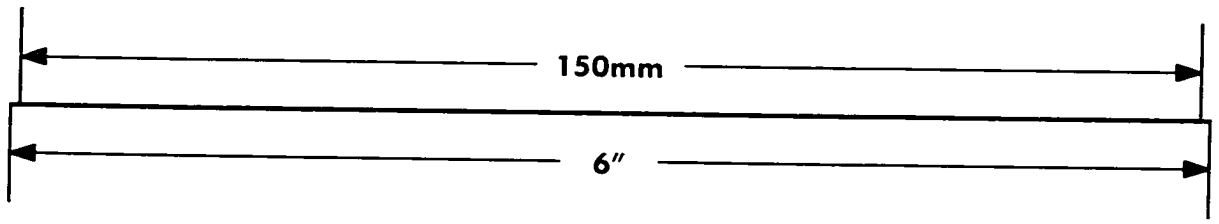
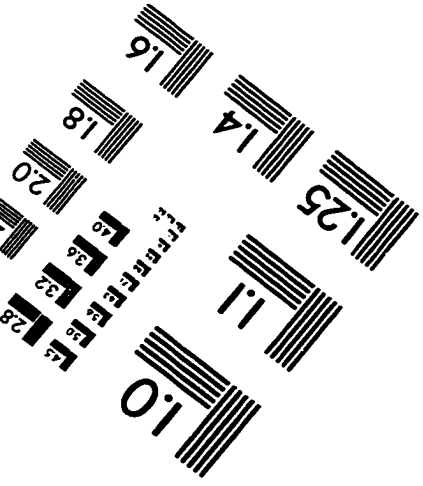
IMAGE EVALUATION TEST TARGET (QA-3)

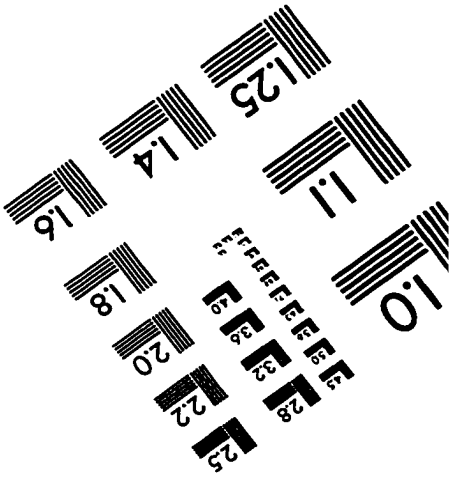












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