Parasite communities of yellow perch (*Perca flavescens* [Mitchill]): patterns, processes and origins of associations

By

Joseph Carney

A Thesis submitted to the Faculty of Graduate Studies in partial fulfilment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

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ABSTRACT

Yellow perch (*Perca flavescens* L) are common fish in the north temperate regions of North America east of the rocky mountains. They occupy multiple trophic levels, feed on what is available and have a large list of parasites recorded of which just one is host specific. As a consequence, they provide a good model system for examining the factors contributing to the development of parasite communities that are unrelated to host specificity. In particular, those factors which might contribute to predictability in the parasite communities and to help determine the origins of the associations between hosts and parasites. This study was conducted to assess if predictability exists in parasite communities lacking host specific parasites at both continental and local scales, and what processes may be responsible for the host-parasite associations and the origins of these associations. Results demonstrated that there was predictability in the continental component communities of both yellow perch in North America and the perch in Eurasia, although the parasites were taxonomically distinct. The parasite communities of these 2 host taxa, which are sister species, are as similar as any of their other biological traits. This predictability extended to the scale of the local component and infracommunities of yellow perch sampled from 5

localities in North America. Within these samples host attributes had little effect on the parasite community richness or abundance. Positive associations between *Proteocephalus pearsei* and *Bothriocephalus cuspidatus* were evident in the Manitoba samples suggesting the possibility of interactions between these species in yellow perch. There was structure in the parasite communities as shown by significant nestedness. Although predictions regarding the effect of lake trophic status on the parasite communities were not supported, trophic status had an indirect effect by limiting the variety of available intermediate hosts. As a result, the predictability in the parasite infracommunities and component communities are best explained by a rich invertebrate community capable of transmitting parasites upon which the perch host feeds. The existence of predictability at both regional and local scales suggested that the core-satellite hypothesis might provide insights into the processes responsible for the observed structure and predictability. The core satellite hypothesis is not supported by the data on yellow perch parasites and therefore does not explain the predictability observed in the communities. Results of cladistic analyses of the family Cucullanidae did not support the previous hypothesis proposed by Petter (1974) but did support the monophyly of the genus *Dichelyne*. It also

did not provide any evidence for cospeciation between *D. cotylophora* and *P. flavescens*. A cladistic analysis of Nearctic species of *Proteocephalus* did not support a hypothesis of cospeciation between the cestode parasites *Proteocephalus pearsei* and *P. percae* and yellow perch and perch, respectively. Evidence supports the interpretation that yellow perch are older than previously thought and did not disperse into North America across Beringia during the Pleistocene. If there was a colonization by dispersal it was across the North Atlantic, although the evidence is more supportive of yellow perch originating in North America. Available evidence supports the interpretation that the parasites predictably associated with yellow perch in North America are a consequence of a host switching with North American endemic fish hosts. Shared feeding habits likely explains the origin of the host capture. Predictability between parasites and hosts does not depend only on host specificity, and can be apparent even for hosts such as yellow perch. Information on the parasite community may predict more about the host and the local environment than does the host and the environment predict about the parasite community.

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GENERAL INTRODUCTION

Processes contributing to the distribution and abundance of species and the structure and composition of communities are central themes of ecology. This theme is expressed first as a search for predictable pattern as demonstrated by repeated species presences, abundances and associations, and habitat and resource utilization, and, second as a search for those processes which may explain the observed patterns. Studies of communities of free-living organisms has shown that communities vary both in their structure and predictability and the processes producing structure. The basis and origins for the association between parasites and their hosts are an extension of this theme.

Parasite community composition and structure in freshwater fishes has received increasing scrutiny in recent years. Explanations have been sought to answer questions concerning differences in community richness among hosts (Aho and Bush, 1993; Kennedy et al., 1986), the relative effects of biotic and abiotic influences (Esch, 1971; Leong and Holmes, 1981), if the communities have structure or are stochastic assemblages (Kennedy, 1990), if parasites interact either intra- or interspecifically (Holmes, 1973; Kennedy, 1985), and the relative importance of contemporary ecological interactions versus historical phylogenetic processes (Bush et al., 1993; Brooks and McLennan, 1991, 1993) as community determinants. These

studies emphasizing different aspects of parasite communities have frequently reached conflicting conclusions resulting in a lack of consensus regarding explanations for fish parasite communities. This absence of consensus has led to the assertion that searching for a central unifying theme explaining freshwater fish parasite community patterns, or parasite communities in general, is futile and that a multifaceted approach is required to address these fundamental questions (Aho and Bush, 1993).

Contributions from parasitology have been largely ignored in the general ecological literature. This has happened even though parasite communities have inherent advantages, including clearly defined community boundaries, replication, recognizable resources, and the possibility of identifying potential interactions among associated species. Furthermore, parasite communities can be defined hierarchically permitting the investigation of scale effects on pattern and process. This hierarchy begins with the parasite community in an individual host, termed the infracommunity (Bush and Holmes, 1986a; Bush et al., 1997), and this is where contemporary species interactions occur. The community of parasites present in a host population, termed the component community (Holmes and Price, 1986; Bush et al., 1997), is a collection of infracommunities. All stages of all parasites present in all hosts in a system are termed the

compound community. The overwhelming majority of studies on parasite communities investigate the infracommunity and component communities.

Parasites of freshwater fishes provide good model systems for the study of parasite communities for several reasons. First, the host occurs in a clearly delineated habitat, i.e. a pond, lake, river, watershed or drainage system. Second, the host can be aged and the effect of size and growth studied, attributes often difficult to determine for many mammals or birds. Third, fish can usually be obtained in sufficient numbers to ensure an adequate sample size for statistical analysis and replication of infracommunities. Fourth, much of the historical development of parasite community ecology derives from studies of freshwater fish parasites. The prevailing theory is that parasite communities of freshwater fishes are stochastic assemblages that are low in richness and are comprised of non-interactive species, that.

The origin of ecological parasitology, especially as it relates to parasite communities of freshwater fishes is found in the early Russian investigations by Dogiel and coworkers (see Dogiel et al., 1958). This was the basis for many of the questions subsequently addressed in later investigations on biotic and abiotic factors considered important in structuring parasite communities of freshwater fishes. In a second major

study, Wisniewski and colleagues (see Wisniewski, 1958) reported on all the parasites in all the hosts in Lake Drzno, Poland. This was a multidisciplinary effort that quantified all the hosts and parasites, the flora, and the abiotic status of the lake and related it to the flow of parasites among hosts. This study has never been duplicated. These studies mark the beginning of modern parasite ecology of freshwater fish and form the basis for the search for repeated patterns in community structure that may have a common cause and the study of parasite ecology in its own right.

By contrast, many of the early studies from North American researchers were influenced by research dealing with the ecology of free-living organisms and were directed more toward a search for processes that might mediate species associations and community structure. In investigations into inter- and intraspecific interactions between and among species in infracommunities, Holmes (1961, 1962) and Bush and Holmes (1986a, 1986b) emphasized competition among parasites as the process for structuring parasite communities. Schad (1963), Holmes (1973) and Rohde (1982) emphasized resource use and niche diversification and segregation. Holmes and Price (1986) identified traits contributing to interactive vs. isolationist community types and Bush and Holmes (1986a), applying the

core-satellite hypothesis of Hanski (1982a), proposed that species belonging in the core mode would be those most likely to interact.

Free-living organisms can give insights into the patterns and processes structuring parasite communities and the study of parasite communities can contribute understanding to communities of free-living organisms. However, parasites by their nature (habitat), are different from free-living organisms and may not be subject to the same influences and constraints, and merit consideration in their own right. As a result, the theories and assumptions relevant to studies of free-living organisms should be cautiously applied to parasite systems. An example of non-productive attempts to follow in the tracks of ecologists studying free-living organisms was the application of the Theory of Island Biogeography (MacArthur and Wilson, 1967) to parasites, with the hosts substituting for islands. A still unresolved issue is the applicability to parasite communities of the core-satellite hypothesis (Hanski, 1982a) developed for communities of free-living organisms.

The majority of these earlier investigations, and their resulting theories are based on the study of ecological processes presently occurring, and, with the exception of "the ghost of competition past", gives only passing consideration to historical and phylogenetic factors. By contrast, Brooks (1988) emphasized the importance of evolutionary events to explain

the association between parasites and their hosts. Brooks (1985) introduced modern systematic methodology, in the form of cladistics, to parasitology and has given many examples of the importance of coevolution in defining the present day associations between parasites and hosts.

The parasite community of yellow perch (*Perca flavescens* [Mitchill]) in North America provides a useful model system to evaluate hypotheses relating to parasite communities in freshwater fishes. Yellow perch are endemic to North America and have a natural range that encompasses much of the temperate zone of North America. As hosts, yellow perch occupy many trophic levels providing numerous opportunities for them to acquire parasites, as evidenced by the more than 90 parasite species reported, of which just one species is specific to yellow perch. Therefore, parasites of yellow perch provide an alternate test of different hypotheses pertaining to parasite community structure which often are evaluated using parasite communities that have a large component of host-specific parasites. Host specificity has been defined differently by numerous researchers; some consider it to be at the level of the single host species while others extend it to include genera and even families of host species. Parasites are always specific to a host, at some taxonomic level, and by extending specificity to include ranks other than single species dilutes the meaning of specificity,

and is inconsistent with the usage employed by researchers studying monogeneans.

The natural range of yellow perch in North America is shown in Figure 1. The sister species to yellow perch is the perch (*Perca fluviatilis* L.) located in Eurasia (Figure 2, page 42). Temperature, current, salinity and oxygen levels limit distributions of each species (Craig, 1987; Thorpe, 1977). Both species have the same pattern of maturation, spawning behaviour, ontogeny, and feeding habits (Thorpe, 1977; Weatherley, 1977; Furnass, 1979; Guma'a, 1979; Mills and Forney, 1981; Craig, 1987; Confer et al., 1990; Carlander, 1997). Growth of both species is affected in the same manner by the same variables of temperature, diet, and competition (Craig, 1987; Carlander, 1997). Although they are recognized as distinct species based on morphology (and geographic discontinuity) they are biologically and ecologically equivalent. Therefore, ecological, behavioural, and physiological results obtained for one species should be applicable to the other.

Since *P. fluviatilis* is the sister species to yellow perch, and is ecologically so similar, it provides the opportunity to compare the parasite communities of these two hosts and to investigate the role of cospeciation as a contributing factor to community structure. Furthermore, comparisons can

be made between these two hosts at the continental scale and between the continental and local scales for yellow perch to assess if there are common patterns across different spatial scales in the parasite communities of yellow perch.

The parasite infracommunities and local component communities of yellow perch are examined to determine the effects of biotic (size, age and sex, feeding and fish community complexity) and abiotic (lake size and trophic status) effects as factors structuring parasite communities. Yellow perch were collected from 2 localities in Manitoba and 3 localities in Wisconsin.

The core-satellite hypothesis (Hanski, 1982a) developed from the study of free-living organisms has frequently been applied to describe parasite communities without being explicitly tested to determine if this model is appropriate. Reasons to examine the core-satellite hypothesis are to test the model using parasite data and to determine if there is a set of "core" species in the different parasite communities that may be a consequence of the processes described using Hanski's model. Are core species host specific and do the hypotheses developed based on free-living organisms have application to fresh water fish parasite communities?

The historical ecology of *P. flavescens* in North America and some of its parasites is examined to determine the origins for the associations between yellow perch and its predictable parasites. A requirement for the study of historical ecology is an estimate of the phylogeny(s) for the taxa being considered, their ancestral origins and a geographic history of the areas involved. Results are interpreted to determine if the parasite fauna in yellow perch resulted from species present during invasion from elsewhere (i.e. yellow perch speciated and dispersed from elsewhere and carried the ancestral parasites along), parasites acquired subsequent to invasion from elsewhere (i.e. yellow perch speciated and dispersed from elsewhere and picked up local parasites) or are they a fauna that developed *in situ* (i.e. yellow perch are ancestrally associated with North America and their parasite fauna represents an association that is a result of this biogeographic ancestral sympatry). This will aid in answering the question of whether the predictable association between some parasite species and yellow perch in North America is due to chance ecological encounters, cospeciation between the host and parasite taxa, or based on historical ecological sympatry among the associated taxa.

I have focused focuses on the parasite communities of yellow perch with regard to answering the following specific objectives. Do common

compositional patterns exist in the parasite communities? Are the parasite communities of yellow perch in North America and perch in Eurasia as similar as their other biological traits and is there predictability (taxonomic or ecological) at the continental scale in the association. Yellow perch from North America were used to determine if the composition of the parasite communities at the local scale could be predicted. If there are identifiable patterns, what processes might be responsible? What biotic and abiotic factors contribute to the infracommunities and component communities of yellow perch and is there any evidence for interaction between or among parasites in the infracommunities of yellow perch? Do the factors structuring yellow perch parasite communities agree with those predictions that the parasite communities of freshwater fish are low in richness, stochastic assemblages that are non-interactive and can parasite data be used to test theories such as the core-satellite hypothesis (Hanski, 1982a) used to explain communities of free-living organisms? What is the origin of yellow perch and what are the origins of the associations between yellow perch and its parasites? Are there repeated patterns in the historical associations between these parasites and yellow perch and are these associations due to cospeciation? These objectives incorporate a multifaceted approach to

determine the patterns, processes and origins of the parasite communities of yellow perch.

CHAPTER 1

Enteric helminths of perch (*Perca fluviatilis* L.) and yellow perch (*Perca flavescens* [Mitchill]): stochastic or predictable assemblages?

ABSTRACT: Component communities of perch (*Perca fluviatilis* L.) in Eurasia and the North American yellow perch (*Perca flavescens* [Mitchill]) were examined to determine the nature of their parasite communities. The scale of this investigation is continental and includes data collected across the distribution of each host species. Data were compiled from the literature and from 5 sample sites in North America. Four parasite species were found to occur frequently in the helminth communities of *P. flavescens*. The cestodes *Bothriocephalus cuspidatus* and *Proteocephalus pearsei*, the digenean *Crepidostomum cooperi*, and the nematode *Dichelyne cotylophora* comprised a suite of species of which some or all occurred in most samples. Similarly, a group of 4 predictable parasite species were identified for *P. fluviatilis* in Eurasia, the digenean *Bunodera luciopercae*, the nematode *Camallanus lacustris*, the cestode *Proteocephalus percae*, and the acanthocephalan *Acanthocephalus lucii*. Specificity was not a requirement for predictability. Despite geographical isolation for millions of years, and different fish species interactions within and between continents, the predictability of these parasite assemblages indicates they are shaped by a biology, especially feeding patterns, common to both perch species. This is evidence that parasite assemblages comprised of non-host-specific parasites

in freshwater fishes are not merely stochastic assemblages, but have key components that are predictable at this broad continental scale.

INTRODUCTION

Whether parasite communities of fish have a predictable structure or are stochastic assemblages is a recurring question in fish parasite community ecology (Dogiel et al., 1958; Holmes, 1990; Kennedy, 1990; Aho and Bush, 1993; Choudhury and Dick, 1998). The apparent unpredictability of species presence or absence in parasite communities of freshwater fish has led Kennedy (1990) to suggest they are stochastic assemblages. By contrast, some researchers consider the structure of parasite communities of freshwater fish to be predictable (Halvorsen, 1971; Wootten, 1973). Whereas Halvorsen (1971) suggested that if a parasite was present in a location it will be predictably associated with a particular host, this does not imply that the presence of a host ensures the presence of a particular parasite species. Holmes and Price (1986), following Wootten (1973), misinterpreted Halvorsen (1971) and implied that a host species in diverse bodies of water will harbor the same parasite species. The prevailing view is that parasite communities of fish are unpredictable and random assemblages, except for those parasites that are host specialists (Choudhury et al., 1996; Choudhury and Dick, 1998). It has been suggested that host-specific parasites should form a predictable set of species within that host's parasite component

community and closely related hosts are expected to share similar parasites (Kennedy and Bush, 1994; Choudhury et al., 1996; Choudhury and Dick, 1998). However, many parasites may be associated with a host for reasons other than host specificity or relatedness among hosts. For instance, host-generalist parasites can be shared among unrelated hosts that have similar ecology or feeding preferences.

Rarely have hosts with few or no host-specific parasites been examined to determine if some parasite species are predictable, based on their frequency of occurrence, over the geographical range of the host. Since host specificity would not be a criterion for predictability of such a parasite component community, the sharing of non-host-specific parasites among related hosts must be the result of common host biological characteristics, or historical ecology, or both.

The perch (*Perca fluviatilis*) from Eurasia and the yellow perch (*Perca flavescens*) from North America now are recognized as sister species (Collette and Banarescu, 1977; Craig, 1987; Shcherbukha, 1993), but have, in the past, been considered conspecific (Svetovidov and Dorofeeva, 1963; Thorpe, 1977). These two species provide an ideal opportunity to examine if host sister species will share enteric parasites to the same degree as other

traits, and if there is predictability in the enteric parasite component community of hosts lacking specific parasites. *Perca fluviatilis* and *P. flavescens* are of further interest since they have similar biological attributes and are widely separated geographically. The latter eliminates sympatry as a confounding factor when assessing for similarities in parasite patterns. There is little likelihood that host specificity will confound the analysis as the only currently recognized parasite specific to yellow perch is the gill monogenean, *Urocleidus adspectus* (Cone and Burt, 1982). My objectives in this chapter are to determine if perch parasite component communities have predictable elements or are stochastic assemblages and if enteric parasites of these two percids are, similar, as are their other shared biological traits. The spatial scale of this investigation is continental and incorporates data across as much of the range of each host species as was available. At this scale, in samples of perch collected from localities across its range, is the probability of a parasite species being present in a sample greater than chance?

MATERIALS AND METHODS

Host specificity is defined as a parasite that reproduces only in 1 host species. I make the distinction between specificity and preference by defining preference as the highest frequency of occurrence of a parasite species in a fish host species. Implicit in this use of preference is the ability of the parasite to reproduce. Furthermore, whereas similarities between parasite component communities are used, where appropriate my final conclusions are based on overall frequency of occurrence. This investigation is at a broad spatial scale i.e., the continental distribution of the hosts. I consider frequencies greater than chance (higher than 50%) to confer predictability at this scale. Although not part of this investigation I am aware that different results may emerge at smaller, more restricted spatial scales.

Sample refers to a collection of hosts from a particular location and year. A component community is defined as all the parasites in a sample of hosts and represents the parasites present in a host population (Holmes and Price, 1986; Bush et al., 1997). Presence or absence in the component community were the only data considered because data for individual hosts are generally lacking. In the present study, it is the association between the parasite species and the host species which is of interest. Richness refers to

the number of parasite species. Mean ($\pm$ SD) species richness is reported where applicable. Spearman rank correlations were calculated using Statview statistical software (Abacus Concepts, 1992) to test if latitude and longitude or sample size had an effect on species richness. Jackknife estimates of species richness were calculated using the computer program RICHNESS as written by Krebs (1989). Matrices were constructed to calculate pairwise comparisons of the number of shared species among all samples for each host species. Pairwise comparisons were made for all parasite species, and for parasite species present in more than 50% of samples.

Data on the enteric parasites associated with *Perca fluviatilis* and *Perca flavescens* compiled from the literature met the following criteria. Hosts had to be collected from a single identifiable locality. The sample location had to be within the present natural range of each host species (Figs. 1, 2). Surveys from translocated or introduced populations were not included. Ten or more hosts of each perch species had to be examined from a single sample site for parasites and samples had to represent most of the natural range of both species. Fresh samples from 2 locations in Manitoba and 3 locations in Wisconsin were also included (Figure 3). Yellow perch

from Dauphin Lake, Manitoba, were collected by standard gang gill and trap nets set near shore in 1.0 - 1.5 m. Fish were collected from mid May through July in 1992 and 1993. Fish from Beaufort Lake, Manitoba, were collected by standard gang gill and trap nets set in 1992 from May to June. Samples from Wisconsin were collected by trawl in July 1993 from Lake Winnebago, southern Green Bay, and Lake Michigan offshore from Milwaukee. All perch were frozen, stored at -20 C following capture, and later necropsied at following standard parasitological methods.

Digeneans and cestodes were fixed in AFA, stained either in aceto-carmine or haematoxylin, cleared in xylene, and mounted in Canada balsam. Nematodes were fixed in hot 70% EtOH and cleared in glycerine for examination as wet mounts. Identifications were made initially using Hoffman (1967) and Schell (1982) and confirmed by reference to the primary literature.

RESULTS

Six parasite species were reported from both host species. Additionally, representatives of 11 genera were shared between the 2 host species (Table 1). No parasite species was specific to either host species.

Perca flavescens enteric parasite component communities are summarized in Table 2. Forty species are reported from 36 samples. Jackknife estimate of total richness was 52 ± 4.62. Observed parasite species richness within samples ranges from 1-15 (mean = 6.4 ± 3.4. The majority of species reported are from 1 or 2 locations only (mean = 5.5 ± 6.2). The most commonly recorded species, each occurring in 19 or more of the samples, are the cestodes *Bothriocephalus cuspidatus* Cooper, 1917 and *Proteocephalus pearsei* La Rue, 1914, the digenean *Crepidostomum cooperi* Hopkins, 1931 and the nematode *Dichelyne cotylophora* Ward and Magath, 1917. One or more of these species occurred in the component community of 30 samples, with all 4 present in 6 samples. The mean number of species shared in pairwise comparisons between all samples was 2.05 ± 1.8. For those 4 species occurring in greater than 50% of samples the mean number shared between all samples was 1.37 ± 1.2.

Perca fluviatilis enteric parasite component communities are summarized in Table 3. Thirty-two species are reported from 39 samples. Jackknife estimate of total richness was 49.5 $\pm$ 5.9. Observed species richness within samples ranged from 1-10 with a mean of 3.8 $\pm$ 2.7. The majority of species reported are from 1 or 2 locations only (mean = 4.8 $\pm$ 7.5). The most commonly recorded species, each occurring in 19 or more of the samples, are *Bunodera luciopercae* (Müller, 1776), the nematode *Camallanus lacustris* (Zoega, 1976), the cestode *Proteocephalus percae* (Müller, 1780) and the acanthocephalan *Acanthocephalus lucii* (Müller, 1776). One or more of these species occurred in the component community of 34 samples, with all 4 present in 13 samples. The mean number of species shared in pairwise comparisons between all samples was 1.6 $\pm$ 1.9. For those 4 species occurring in greater than 50% of samples the mean number shared between all samples was 1.37 $\pm$ 1.0.

There was no statistically significant correlation between either latitude or longitude and parasite species richness. There was a positive correlation between richness and sample size for the North American samples ($r_S = 0.37$, $P = 0.02$) and the Eurasian samples ($r_S = 0.58$, $P = 0.001$).

DISCUSSION

Parasite component communities of freshwater fishes are considered to be unpredictable stochastic assemblages (Kennedy, 1990) or predictable across geographic or limnologic boundaries (Halvorsen, 1971; Wootten, 1973). The former is based primarily on data from the British Isles (Kennedy, 1990; Hartvigsen and Kennedy, 1993; Kennedy, 1993) and may reflect the effects of anthropogenic activity. By contrast, Halvorsen (1971) suggested that fish parasites would be predictably associated with a host species across a range of locations and Choudhury and Dick (1998) suggested predictability is strongest if there is host specificity. The purpose of the present investigation was to evaluate the enteric helminth component communities of 2 percids, known to have broad ecological requirements across continents, and considered to harbor few, if any, host-specific parasites. Whereas I have defined host specificity in a very strict manner I recognize that some parasite species may occur most frequently in a particular host species despite being found in a number of other host taxa.

Initial observations of the data from this study revealed that the enteric parasite component communities of yellow perch and European perch are similar in pattern, but taxonomically different. The fact that the majority of

parasite species occurred with low frequency, in both hosts, contributes to this similarity. Of the 43 enteric species reported from yellow perch in North America, 11 species are reported only from single samples and may represent acquisitions from a preferred sympatric host species. This may be a consequence of sampling effort. Of the 11 species unique to single samples, 6 came from collections of over 200 fish with 4 of these coming from a single study (Szalai, 1989; Szalai et al., 1992). It is possible that these unique species may be present in more of the samples but are unrecorded due to small sample size. This could result in additional species being added to the suite of parasites considered predictable across the continental distribution of yellow perch. Furthermore, parasites that are rare at the continental scale of this investigation, may be common in perch at the local scale. A similar pattern is observed for the 32 species of parasites from perch in Eurasia with 17 species reported from single samples. The same considerations discussed above for yellow perch in North America applies to perch in Eurasia.

Although the majority of parasite species are unique to each continent, some taxonomic overlap exists among the parasite species in the 2 percids. For example, 6 parasite species, *Crepidostomum farionis* (Müller, 1784), *C. metoecus* (Braun, 1900), *Bunodera lucioperca*, *Camallanus truncatus*

(Rudolphi, 1914), *Echinorhynchus salmonis* Müller, 1784, and *Neoechinorhynchus rutili* Mueller, 1780 are reported from the 2 hosts on both continents (Table 1). It is not surprising that *Crepidostomum farionis* and *C. metoecus* occur with low frequency in percids since they are typically salmonid parasites (Hoffman, 1967; Margolis and Arthur, 1979). The presence in the 2 perch hosts of *Camallanus truncatus*, *E. salmonis* and *N. rutili* is likely due to their wide distribution and lack of host specificity (Bykhovskaya-Pavlovskaya et al., 1962; Hoffman, 1967; Margolis and Arthur, 1979). *Bunodera lucioperca* is most frequently reported from percids but also infects a large number of other fish hosts (Bykhovskaya-Pavlovskaya et al., 1962; Hoffman, 1967; Margolis and Arthur, 1979), indicating the importance of shared species of host in the maintenance of a parasite population.

Sympatry of perch with other fish species is the source of many species of parasites, especially those occurring at low frequency in *P. flavescens* and *P. fluviatilis* and indicates that other fish species influence the parasite community of both perch species. For example, *Azygia angusticauda* is frequently reported from pike in North America and is occasionally reported from *P. flavescens*. Similarly, different species of

Bucephalus, *Rhipidocotyle*, *Bothriocephalus*, and *Pomphorhynchus* occur rarely in the 2 perch hosts and frequently in other fish species from Eurasia and North America (Table 1).

Combining the above observations could lead one to conclude that the perch parasite component communities are stochastic. However, a more careful evaluation of the data clearly indicates there is a portion of the component community that occurs with high frequency, indicating a degree of predictability previously unnoticed even though the individual parasite species are not host-specific and usually differ between the 2 percid species. Although taxonomically different, these parasites species have similar ecologies, including mode of transmission and patterns of host preference.

In the *P. flavescens* component community, 4 parasite species (*P. pearsei*, *B. cuspidatus*, *C. cooperi*, and *D. cotylophora*) occur at a frequency greater than 50%. A good example to illustrate the difference between specificity and preference is shown by *P. pearsei* and *D. cotylophora*, which are reported most frequently from yellow perch, but also from many other fishes (Hoffman, 1967; Margolis and Arthur, 1979). Even in a depauperate enteric component community, 1 of these frequently occurring parasites, *P. pearsei,* was the only enteric species in a sample from Ohio (Bangham,

1941). *Bothriocephalus cuspidatus* has a large list of reported hosts (Hoffman, 1967) and *Crepidostomum cooperi* is notable for its lack of host specificity (Caira, 1989). Clearly, host specificity is not a requirement for inclusion in the suite of parasite species expected to be present in the parasitofauna of yellow perch. Although the number of species shared between all samples is low, the majority of that similarity results from the presence of these 4 species in the samples.

Interestingly, 6 of the 36 samples (16%) had none of the 4 species in the component community. In the case of *D. cotylophora*, its absence from 8 samples in the Hudson Bay drainage (Poole, 1985; Szalai, 1989; Szalai et al., 1992; this study) and presence in the Great Lakes drainage can be explained by its persistence in an ancestral geographical area (Great Lakes) and dispersal into a previously glaciated region by the fish host without the parasite. *Dichelyne cotylophora* is even more common, and therefore predictable, in yellow perch component communities if only samples outside of the Hudson Bay drainage are considered. Whereas this highlights the effect of scale, it does not compromise the pattern shown by those parasite species found at high frequency throughout the range of perch.

There are 4 species of parasites (*B. luciopercae*, *Camallanus lacustris*, *P. percae*, and *A. lucii*) occurring in more than 50% of the component communities of *P. fluviatilis*. These species also represent the majority of species shared between all samples (Table 3) . None of these 4 species are host-specific, all are commonly reported from many host species (Bykhovskaya-Pavlovskaya et al., 1962; Bauer, 1987), but all are reported most frequently from perch.

Although taxonomically different from those species reported from *P. flavescens*, there is a suite of frequently occurring parasites in *P. fluviatilis* which are not host-specific. This is further support for the contention that factors other than host specificity affect the parasite component community composition of both hosts. One of these factors appears to be the generalist parasite communities of holarctic fishes which help shape the parasitofauna of perch on both continents. Since perch feed across most trophic levels, they readily acquire parasites from this generalist parasite community.

The unspecialized ecological requirements of perch (Thorpe, 1977; Craig, 1987) are reflected in their feeding patterns which may influence the transmission of enteric helminths. The parasite species occurring with greatest frequency in the 2 percid hosts, although taxonomically different,

show similarities in their route of transmission. For example, *P. flavescens* has the cestodes *P. pearsei* and *B. cuspidatus*, whereas *P. fluviatilis* has the cestode *P. percae* and the nematode *C. lacustris*. All these parasites are transmitted by copepods (Essex, 1928; Freze, 1965; Amin, 1978; Moravec, 1994), a frequent item in the diet of both hosts (Craig, 1987). Furthermore, *P. flavescens* has the digeneans *C. cooperi* and *B. sacculata*, whereas the digenean *B. luciopercae* and the acanthocephalan *A. lucii* occur in *P. fluviatilis*. All these species of parasites are transmitted by benthic macroinvertebrates (Choquette, 1954; Bykhovskaya-Pavlovskaya et al., 1962; Cannon, 1971). *Dichelyne cotylophora* is transmitted by piscivory to *P. flavescens* (Baker, 1984), but there is not a comparable species in *P. fluviatilis*, even though it is piscivorous (Thorpe, 1977; Craig, 1987). In fact, there is no frequently occurring parasite of *P. fluviatilis* which is transmitted by piscivory.

Although the overall pattern of parasitism between the 2 host species is similar, there are differences worth noting. Total parasite species, and total and mean sample richness, were higher for *P. flavescens* than for *P. fluviatilis*. When host-parasite lists are compared (Bykhovskaya-Pavlovskaya et al., 1962; Hoffman, 1967; Margolis and Arthur, 1979), *P.*

flavescens has more parasite species than *P. fluviatilis*. This is contrary to what is expected since *P. fluviatilis* has a much wider geographic range and it has been suggested that host species with large geographic ranges will have more parasite species in total than host species with a comparatively restricted spatial distribution (Price and Clancy, 1983; Gregory, 1990; Guegan and Kennedy, 1993). Feeding habits alone cannot explain the higher parasite richness in *P. flavescens* since they are similar for both host species. However, as there are more fish species sympatric with yellow perch in North America than with perch in Eurasia, this provides a greater number of host species with which to share parasites.

There is a substantial stochastic aspect to the parasitofauna of North American and Eurasian perch which is reflected in the large number of parasites recorded at low frequency across their geographic ranges. The presence of these parasites in the component community reflects local factors, especially the presence of other fish hosts with which parasites can be shared. However, there is also a predictable aspect to the parasitofauna of *P. flavescens* and *P. fluviatilis* indicated by the high frequency of occurrence by members of a suite of parasites which reflects their feeding habits and other interspecific interactions. These enteric parasites are as predictable as

other biological traits. For example, both perch species have virtually identical feeding habits (Craig, 1987), but feed on taxonomically different items on each continent. The enteric parasitofauna of both are remarkably similar, but are comprised mostly of taxonomically different species. Since the hosts are sister taxa one would expect taxonomically similar parasite species due to phylogenetic inheritance, but this is not the case. As sister taxa, both percids have similar feeding ecology, habitat requirements, behavior, and physiology. Because of these inherited similarities, they acquire ecologically similar, but taxonomically distinct, parasites which nevertheless are predictable. The predictability and similarity of their parasitofauna indicates that in spite of being separated geographically for millions of years, the hosts have retained a remarkably similar ecology of which the parasite component community is a part. We now know that even within fish hosts such as perch, with a very broad range of ecological requirements and an impressive list of non-host-specific parasites, a major part of perch parasite component communities is shaped by historical ecological events and is not simply a stochastic assemblage, at this broad continental scale.

Table 1. Enteric parasite genera and species shared between *Perca flavescens* and *Perca fluviatilis*. Transmission route to perch and known parasite distribution are indicated.

Genera and species shared	Typical* North American host	Typical Eurasian host	Route of transmission	Distribution
Digenea				
Bunodera				
B. lucioperca	*Perca* + many fish spp.	Percidae spp.	*Daphnia, Hyalella*	Holarctic
B. sacculata	*Perca* + others		*Daphnia*	North America
Crepidostomum				
C. farionis	Salmonidae spp.	Salmonidae spp.	*Ephemera*, Amphipoda, gammarid	Holarctic
C. metoecous	Salmonidae spp.	Salmonidae spp.	chironomid larvae	North America, Europe
C. isostomum	Percidae spp. + Percopsidae spp.		mayfly larvae	North America
C. cooperi	numerous		mayfly larvae, Amphipoda	North America
Azygia				
A. angusticauda	*Esox* spp.+ others			North America

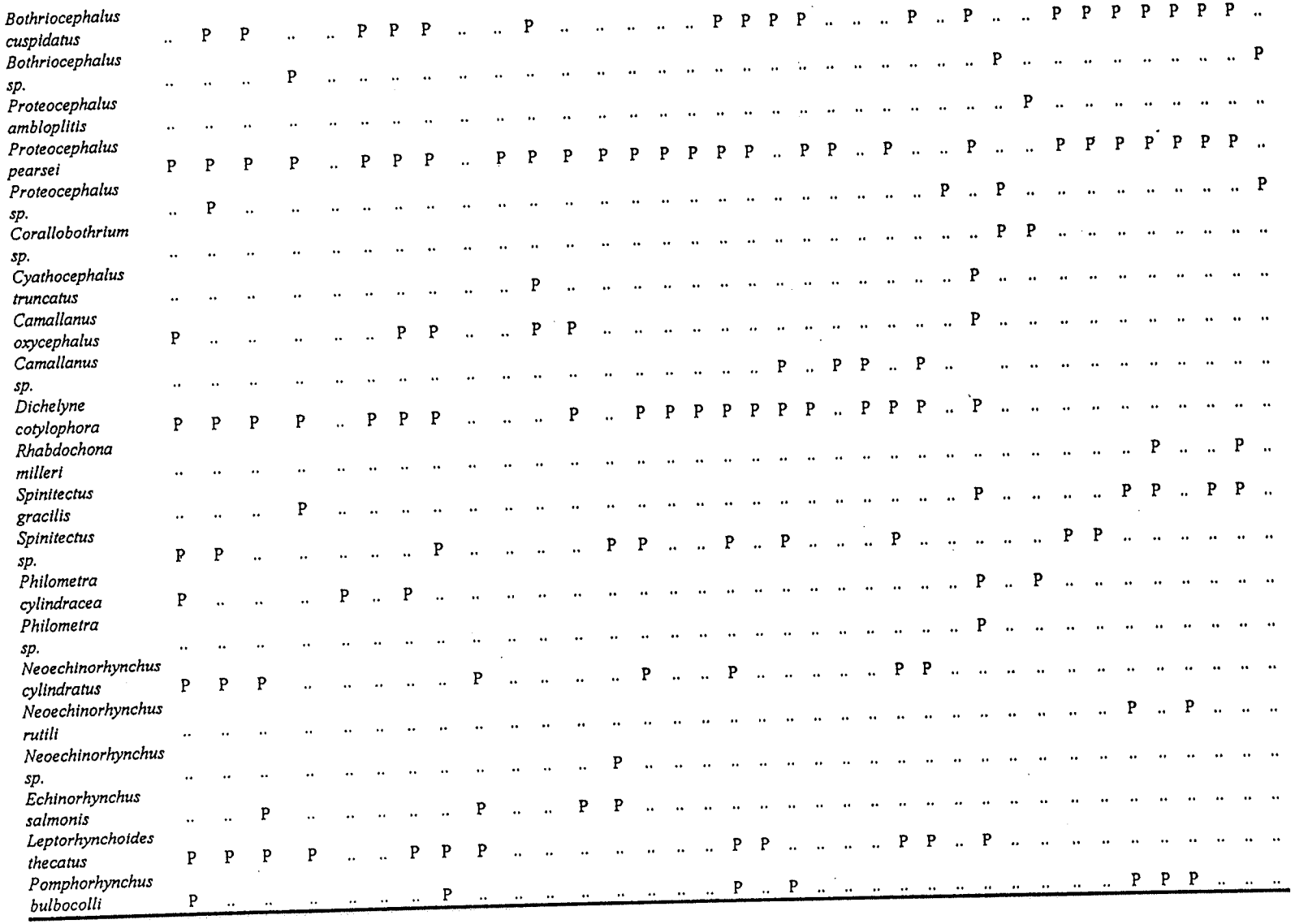
A. lucii		*Esox* spp. + others		Eurasia
Bucephalus				
B. elegans	Centrarchidae spp. + others		fish ingestion	North America
B. polymorphus		numerous	fish ingestion	Eurasia
Rhipidocotyle				
R. papillosa	Centrarchidae spp.		fish ingestion	North America
R. illense		*Esox* + others	fish ingestion	Eurasia
Cestoda				
Bothriocephalus				
B. cuspidatus	*Stizostedion* spp.		copepod ingestion	North America
B. claviceps	Centrarchidae spp.		copepod ingestion	North America, Europe
B. scorpii		marine Cottidae spp.	copepod ingestion	Eurasia
Proteocephalus				
P. ambloplitis	Centrarchidae spp.		copepod ingestion	North America
P. pearsei	*Perca* + others		copepod ingestion	North America
P. cernuae		*Perca* + others	copepod ingestion	Eurasia
P. percae		*Perca* + others	copepod ingestion	Eurasia

P. torulosus		Cyprinidae spp.	copepod ingestion	Eurasia
Nematoda				
Camallanus				
C. oxycephalus	numerous		copepod ingestion	North America
C. truncatus	Centrarchidae spp.	numerous	copepod ingestion	Holarctic
C. lacustris		Percidae (?) + others	copepod ingestion	Eurasia
Acanthocephala				
Echinorhynchus				
E. salmonis	numerous	numerous (Salmonidae?)	amphipod ingestion	Holarctic
E. clavula		numerous	amphipod ingestion	Eurasia
Neoechinorhynchus				
N. cylindratus	numerous		fish ingestion (?)	North America
N. rutili	numerous	numerous	amphipod ingestion	Holarctic
Pomphorhynchus				
P. bulbocolli	numerous (Catostomidae?)		amphipod, fish ingestion	North America
P. laevis		numerous (Cyprinidae?)	amphipod ingestion	W. Eurasia

*Typical refers to the host reported with greatest frequency as determined from checklists (Hoffman, 1967; Margolis and Arthur, 1979; Bykhovskaya-Pavlovskaya et al., 1962)

Table 2. Parasitological surveys of *Perca flavescens* from North America. Enteric species only.

Source*	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
Sample size	273	54	634	1310	20	24	45	93	150	17	38	107	95	41	11	16	21	18	27	12	10	17	12	10	69	67	11	292	265	99	201	63	78	40	11	60
Species richness	15	13	9	8	2	5	10	10	3	1	5	4	5	5	4	4	10	5	9	4	3	5	8	6	2	11	3	7	6	4	11	8	6	4	5	3
Parasite																																				
Lissorchis kritskyi	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	P	..	..	..	..	..	..	P	..	..	..	..	..
Azygia angusticauda	P	P	..	..	P	..	..	P	..	..	..	..	..	..	..	P	P	..	P	..	..	P	P	..	..	..	..	..	..	..	..	..	..	..	..	..
Azygia longa	..	..	..	..	..	..	P	P	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Leuceruthrus sp.	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	P	..	..	..	..	..	..	..	..
Bucephalopsis pusillum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	P	..	..	..	..	..	..	..	..	..	..	..
Bucephalus elegans	P	P	..	..	..	..	..	P	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Prosorhynchoides pusilla	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	P	..	..	..	..	..
Rhipidocotyle papillosus	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	P	P	..	..	..	..
Centrovarium lobotes	P	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	P	..	..	..	..	..	..	..
Cryptogonimus chyli	..	..	..	..	..	..	P	..	..	..	..	..	..	..	..	..	..	..	P	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Allacanthochasmus sp.	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	P	..	..	..	..	..	..	..	..
Neochasminae *sp.*	..	P	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Microphallus opacus	..	..	..	..	..	..	P	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Bunodera luciopercae	P	..	P	P	..	P	..	..	..	..	..	..	P	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	P	..	..	..	..	..	P†
Bunodera sacculata	P	P	P	P	..	..	..	..	..	..	..	..	..	..	P	P	P	..	P	P	P	P	P	..	..	P	..	..	..	..	P	P	P	P	..	..
Crepidostomum cooperi	P	P	P	P	..	..	P	P	..	..	P	..	..	P	P	..	P	P	P	..	..	P	P	..	..	..	..	..	P	..	P	P	P	..	P	..
Crepidostomum farionis	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	P	..	..	..	..	..
Creptotrema funduli	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	P	..	..	..	..	..	..	..
Phyllodistomum superbum	P	P	..	..	..	..	..	..	..	..	..	..	..	..	..	..	P	..	P	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..

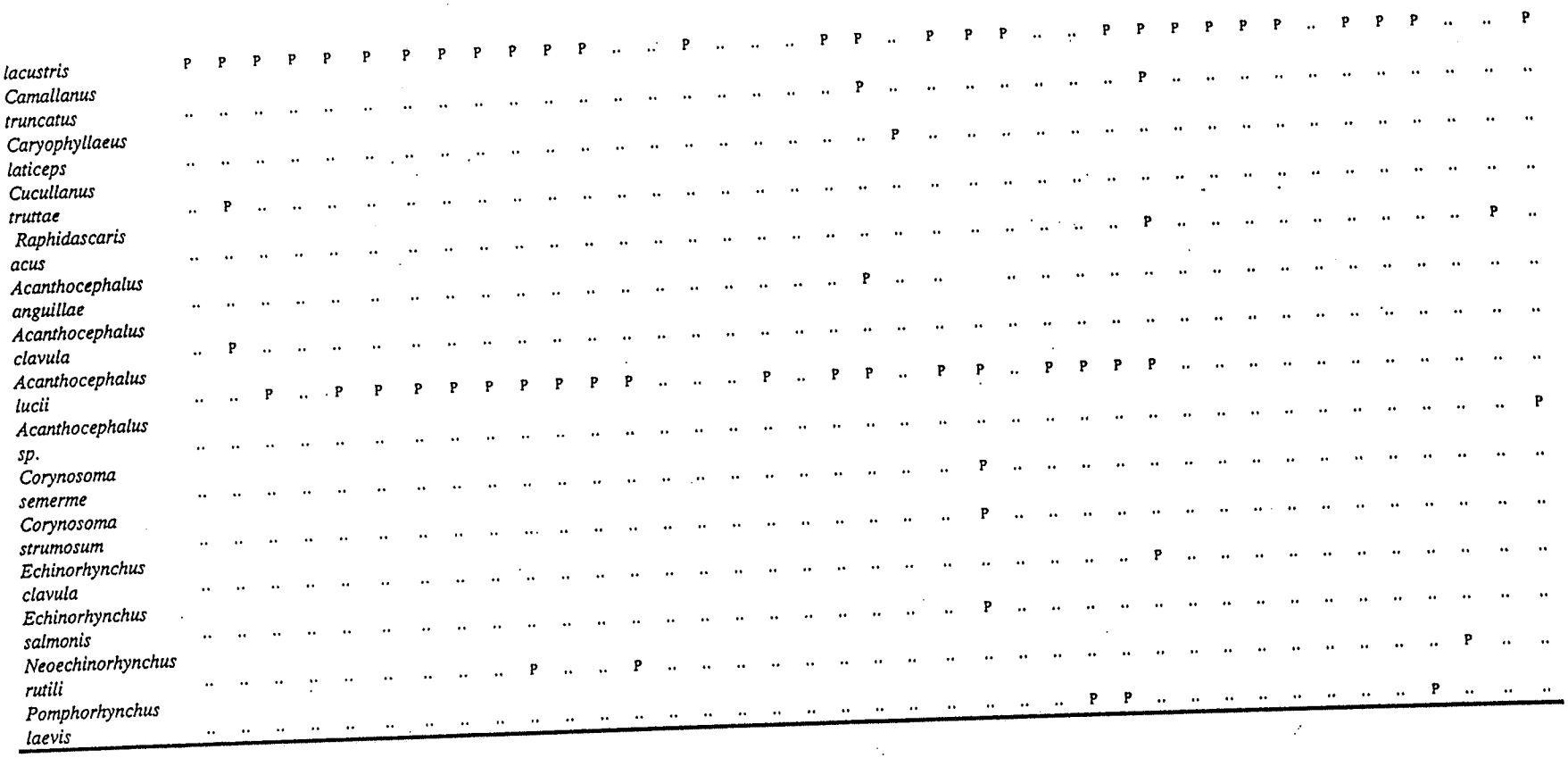

Bothriocephalus cuspidatus
Bothriocephalus sp.
Proteocephalus ambloplitis
Proteocephalus pearsei
Proteocephalus sp.
Corallobothrium sp.
Cyathocephalus truncatus
Camallanus oxycephalus
Camallanus sp.
Dichelyne cotylophora
Rhabdochona milleri
Spinitectus gracilis
Spinitectus sp.
Philometra cylindracea
Philometra sp.
Neoechinorhynchus cylindratus
Neoechinorhynchus rutili
Neoechinorhynchus sp.
Echinorhynchus salmonis
Leptorhynchoides thecatus
Pomphorhynchus bulbocolli

Sources for data on parasitological surveys of *Perca flavescens* from North America presented in Table 2.

*Source. 1: van Cleave & Mueller, 1934 Oneida Lake, NY (43°N 76°W). 2: Noble, 1970. Oneida Lake, NY (43°N 76°W). 3. Tedla and Fernando, Lake Ontario (44°N 77°W). 4: Cannon, 1973. Lake Opeongo, Ont. (45°N 78°W). 5: Molnar et al., 1974. Laurel Creek, Ont. (43°N 80°W). 6: Bangham & Hunter, 1939. E. Lake Erie (43°N 80°W). 7: Bangham & Hunter, 1939. W. Lake Erie (42°N 83°W). 8: Bangham, 1972. Lake Erie (42°N 83°W). 9: Dechtiar, 1972, Lake Erie (42°N 83°W). 10: Bangham, 1941. Buckeye Lake, OH (40°N 83°W). 11: Carney & Dick, this study. Lake Michigan (44°N 87°W). 12: Carney & Dick, this study Green Bay, WI (45°N 87°W). 13: Carney & Dick, this study. Lake Winnebago, WI (45°N 87°W). 14: Bangham, 1944. Madeline Lake, WI (45°N 89°W). 15: Bangham, 1944. Carroll Lake, WI (45°N 89°W). 16: Bangham, 1944. Snake Lake, WI (45°N 89°W). 17: Bangham, 1944. Sweeney Lake, WI (45°N 89°W). 18: Bangham, 1944. Clear Lake, WI (45°N 89°W). 19: Bangham, 1944. Johnson Lake, WI (46°N 89°W). 20: Bangham, 1944. Little John Lake, WI (46°N 89°W). 21: Bangham, 1944. Nebish Lake, WI (46°N 89°W). 22: Bangham, 1944. Pinkeye Lake, WI (46°N 89°W). 23: Bangham, 1944. White Sand Lake, WI (46°N 89°W). 24: Bangham, 1944. Chetac Lake, WI (46°N 91°W). 25: Meyer, 1958. Turnbull Lake, IA (43°N 95°W). 26: Dechtiar, 1972a. Lake of the Woods, Ont. (49°N 95°W). 27: Sutherland & Holloway, Jr., 1979. Missouri River, ND (47°N 101°W). 28: Szalai, 1989. Dauphin Lake, Man. (51°N 99°W). 29: Carney & Dick, this study. Dauphin Lake, Man. (51°N 99°W). 30: Carney & Dick, this study. Beaufort Lake Man. (50°N 100°W). 31: Poole, 1985. Heming Lake, Man. (55°N 101°W). 32: Poole, 1985. Wapun Lake, Man. (55°N 101°W). 33: Poole, 1985. Home Lake, Man. (55°N 101°W). 34: Poole, 1985. Demarch Lake, Man. (55°N 101°W). 35: Poole, 1985. Quigley Lake, Man. (55°N 101°W). 36: Zelmer & Arai, Garner Lake Alta. (54°N 111°W).

Table 3. Parasitological surveys of *Perca fluviatilis* from Eurasia. Enteric species only.

Source*	1	2	3	4	5	6‡	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39
Sample size	181	559	611	62	201	>30	115	120	119	90	504	311	64	74	35	17	18	17	373	533	322	>30	30	12	17	†	†	28	21	65	29	13	19	16	14	50	48	>30	276
Richness	3	7	4	1	5	4	6	6	6	10	6	4	5	1	1	0	1	0	5	6	3	7	10	1	3	6	8	10	2	3	1	1	0	3	2	4	5	1	5
Parasite																																							
Azygia lucii	..	..	..	..	..	..	P	P	P	P	P	..	P	..	..	..	..	..	..	..	..	P	P	..	..	..	..	P	..	P	..	..	..	..	..	..	P	..	..
Bucephalus polymorphus	..	..	..	..	..	..	..	P	P	P	..	..	..	..	..	..	..	..	..	..	....	..	P	..	..	P	P	P	..	P	..	..	..	P	..	..	..	..	..
Bunodera luciopercae	P	P	..	..	P	P	P	P	P	P	P	P	P	..	..	..	..	..	P	P	P	P	P	..	P	P	P	P	P	..	..	..	..	P	P	P	P	..	P
Crepidostomum farionis	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	P	..	..
Crepidostomum metoecus	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	P	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Crowcrocaecum skrjabini	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	P	P	P	P	..	..	..	..	..	..	..	..	..	..	..
Nicolla skrjabini	..	..	..	..	..	..	..	..	..	P	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Rhipidocotyle illense	..	..	P	..	..	..	P	..	..	P	P	..	..	..	..	..	..	..	..	..	..	P	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	P
Bothriocephalus claviceps	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	P	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Bothriocephalus sp.	..	P	..	..	P	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Bothriocephalus scorpii	..	..	..	..	..	..	..	..	..	P	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Cyathocephalus truncatus	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	P	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Eubothrium sp.	..	P	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Proteocephalus cernuae	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	P	..	..	..
Proteocephalus percae	P	..	P	..	P	P	P	P	P	P	P	P	P	P	..	..	..	..	P	P	P	P	P	..	..	..	P	P	..	..	..	..	..	..	..	..	P	..	P
Proteocephalus torulosus	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	P	P	..	..	..	..	..	..	..	..	..	..	..	..
Proteocephalus sp. Camallanus	..	P	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..


lacustris
Camallanus truncatus
Caryophyllaeus laticeps
Cucullanus truttae
Raphidascaris acus
Acanthocephalus anguillae
Acanthocephalus clavula
Acanthocephalus lucii
Acanthocephalus sp.
Corynosoma semerme
Corynosoma strumosum
Echinorhynchus clavula
Echinorhynchus salmonis
Neoechinorhynchus rutili
Pomphorhynchus laevis

Sources for data on parasitological surveys of *Perca fluviatilis* from Eurasia presented in Table 3.

*Source.1: Wootten, 1973. Hanningfield Res., Essex, England (51°N 0°29'E). 2: Andrews, 1979. Llyn Tegid, Wales (53°N 3°W). 3: Lee, 1977. London, England (51°N 0°07'W). 4: Kennedy & Burrough, 1978. Malham Tarn, England (54°N 2°W). 5: Mishra & Chubb, 1969. Shropshire Canal, England (53°N 2°W). 6: Chubb, 1970 Rostherne Mere, England (53°N 2°W). 7: Wisniewski, 1958; Kozicka, 1959. Druzno Lake, Poland (54°N 19°E). 8: Pojmanska et al., 1980. Konin Lakes, Poland (52°N 18°E). 9: Pojmanska et al., 1980. Goplo Lake, Poland (52°N 19° E). 10: Rockicki, 1975. Gdansk Bay, Poland (54°N 18°E). 11: Wierzbicki, 1971. Lake Dargin, Poland (54°N 21°E). 12: Andersen, 1978. Lake Royetjern, Norway (60°N 11°E). 13: Halvorsen, 1971. Glomma River, Norway (59°N 11°E). 14: Lucky & Navratil, 1984. Hubenov Reservoir, Czechoslovakia (49°N 16°E). 15: Lucky & Navratil, 1984. Landstejn Reservoir, Czechoslovakia (49°N 16°E). 16: Lucky & Navratil, 1984. Ludkovice Reservoir, Czechoslovakia (49°N 16°E). 17: Lucky & Navratil, 1984. Mostiste Reservoir, Czechoslovakia (49°N 16°E). 18: Lucky & Navratil, 1984. Opatovice Reservoir, Czechoslovakia (49°N 16°E). 19: Scholz, 1986. Macha Lake, Czechoslovakia (50°N 14°E). 20: Priemer, 1979. Berlin, Germany (52°N 13°E). 21: Ozcelik & Deufel, 1989. Bodensee, Germany (47°N 9°E). 22: Rauckis, 1977. Lithuania (54°N 24°E). 23. Barysheyva & Bauer, 1957. Lake Ladoga, Russia. (61°N, 31°E). 25: Kulakovskaya, 1960. Prut River, Ukraine (48°N 25°E). 25: Marits, 1957. Prut River, Moldavia (46°N 28°E). 26. Kulakovskaya, 1959. Prut River, Ukraine (48°N 25°E). 27. Kulakovskaya, 1959. Dnestr River, Ukraine (48°N 28°E) 28: Shevchenko, 1956. Donets River, Ukraine (48°N 40°E). 29: Ivanov, 1933. L. Volga River, Russia (48°N 40°E). 30: Sidorov, 1956. Lake Soozhargan, Kazakhstan (49°N 63°E). 31: Sidorov, 1956. Lake Dzalangash, Kazakhstan (49°N 63°E). 32: Agapova, 1960. Tobol River, Kazakhstan (53°N 63°E). 33: Agapova, 1960. Obagon River, Kazakhstan (53°N 63°E). 34: Sidorov, 1957. Lake Kurgal′ dzhin, Kazakhstan (50°N 70°E). 35: Bychovsky, 1936. Ubinskoye Lake, Russia (55°N 79°E). 36: Bykhovsky, 1936. Sartlan Lake, Russia (55°N 80°E). 37: Spasskii & Roitman, 1960. Upper Yenisey River, Russia (52°N 97°E). 38: Dogiel & Volkova, 1957. Lake Baikal, Russia (53°N 108°E). 39: Tarmakhanov, 1987. Lake Baikal, Russia (53°N 108°E).

† Actual sample size not indicated. Based on 1502 fish representing 36 species.
‡ Based on Rivdi PhD thesis.

Figure 1. Locations of yellow perch (*Perca flavescens*) samples in North America. Shaded area indicates natural range of yellow perch (after Craig, 1987). Numbers refer to samples in Table 2.

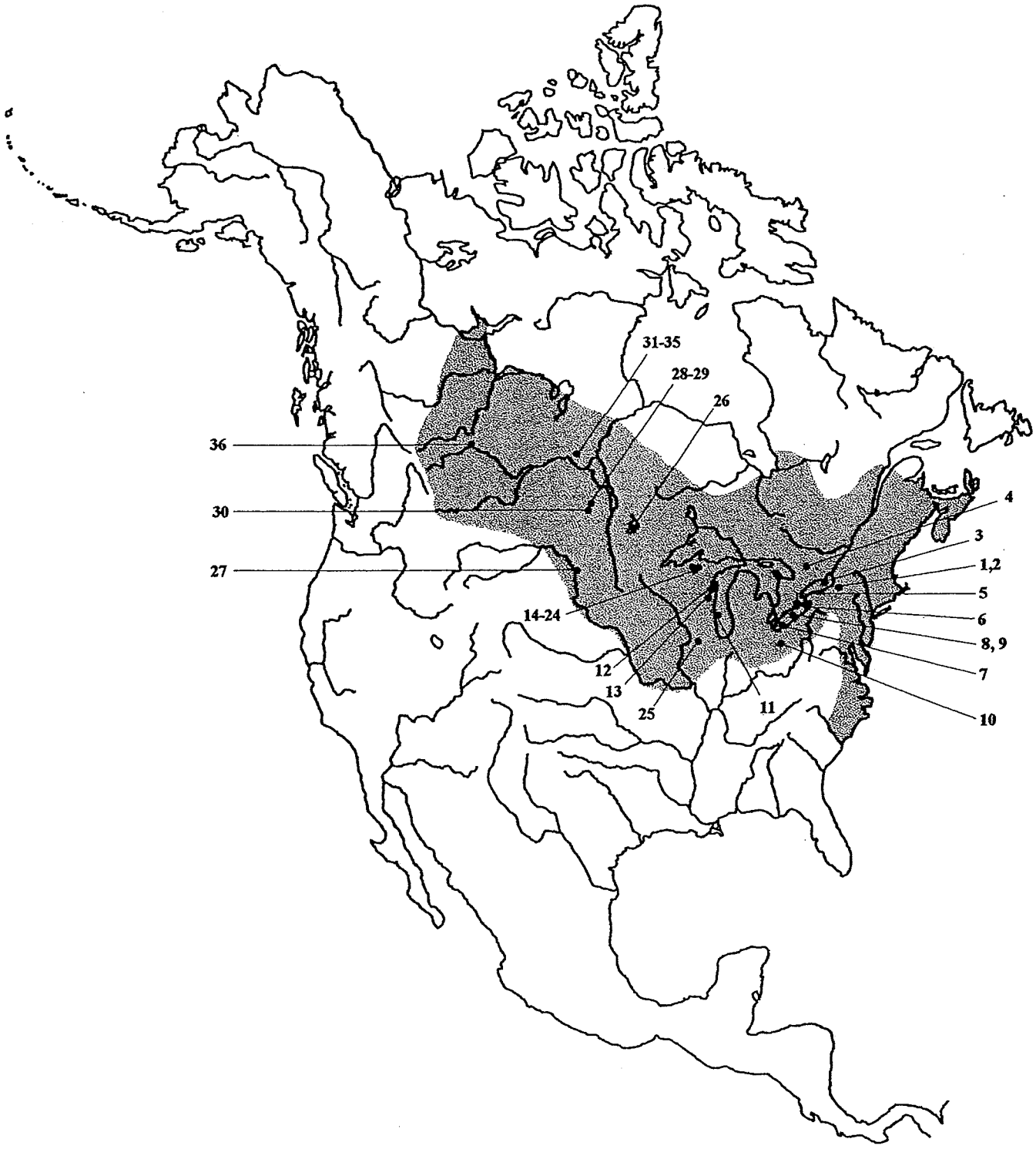
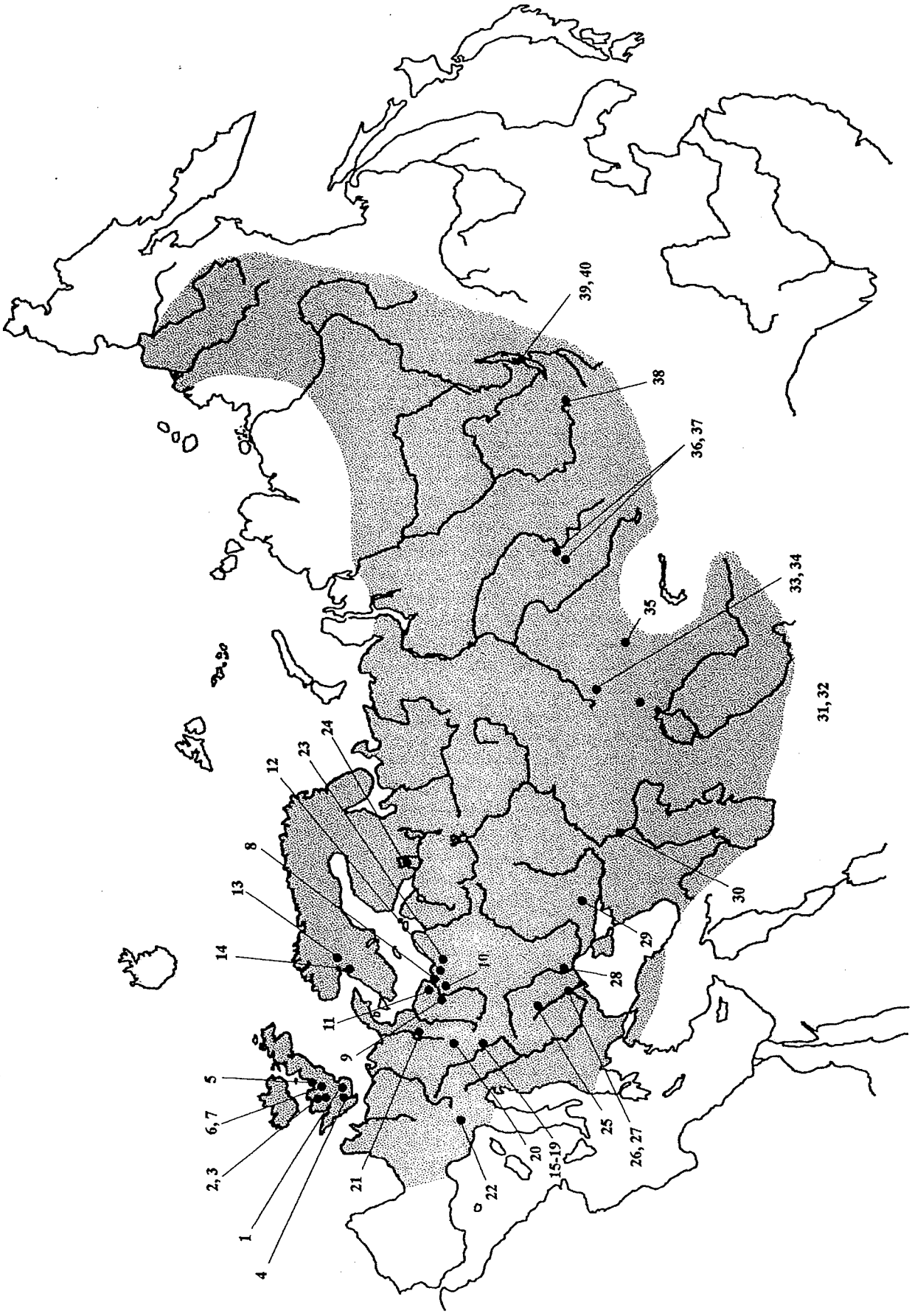

31-35
28-29
26
36
30
27
4
3
1,2
5
6
8, 9
7
10
14-24
12
13
25
11

Figure 2. Locations of perch (*Perca fluviatilis*) samples in Eurasia. Shaded area indicates natural range of perch (after Craig, 1987). Numbers refer to samples in Table 3.


39, 40
38
36, 37
33, 34
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31, 32
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12
8
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14
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6, 7
2, 3
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22
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15-19
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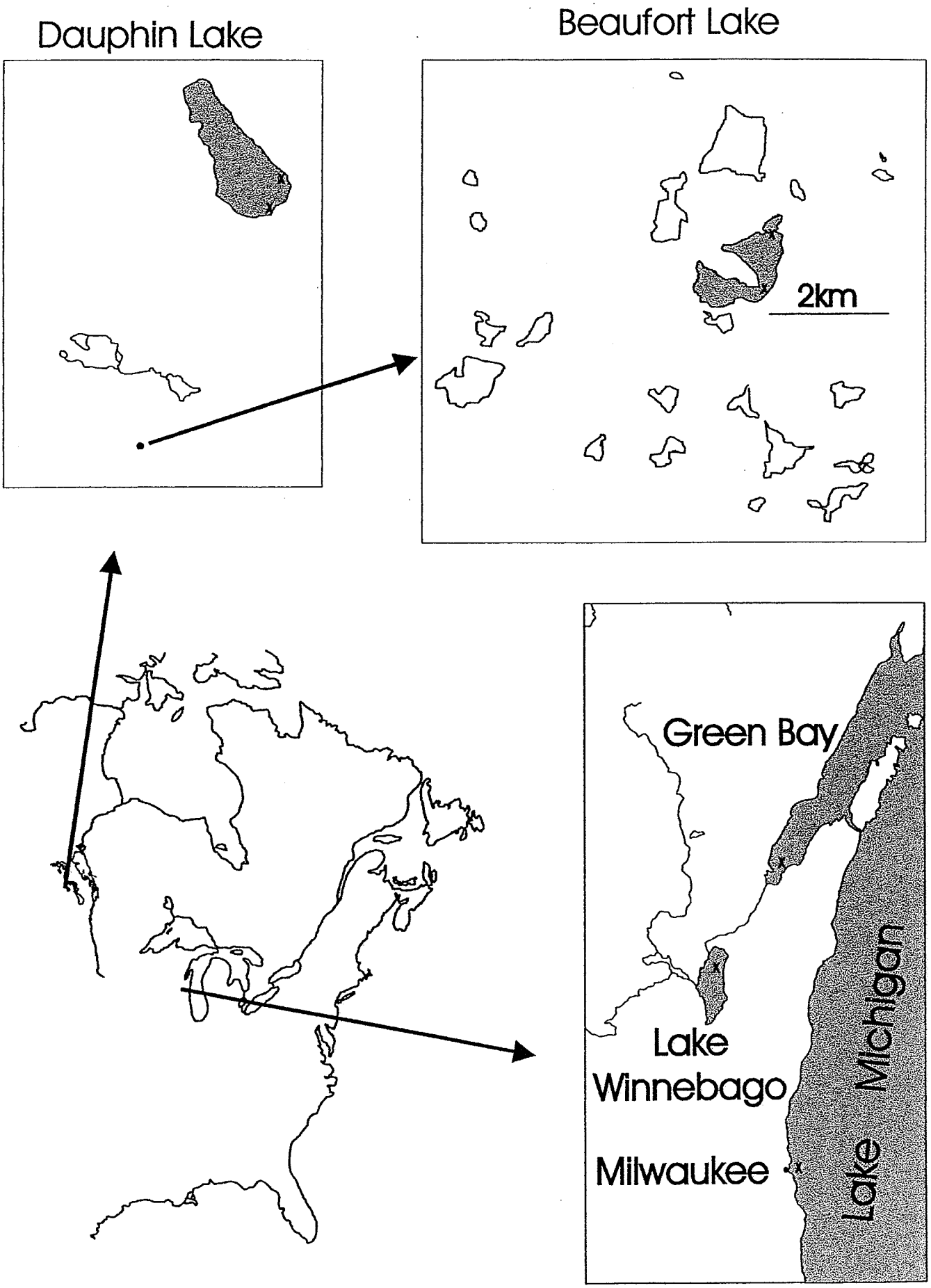
26, 27

Figure 3. Locations of the samples collected from Dauphin Lake and Beaufort Lake, Manitoba, and Lake Winnebago, Green Bay and Lake Michigan, Wisconsin.


Dauphin Lake
Beaufort Lake
2km
Green Bay
Lake
Winnebago
Milwaukee
Lake Michigan

CHAPTER 2

Helminth assemblages of yellow perch (*Perca flavescens* [Mitchill]): determinants of pattern.

ABSTRACT: Twenty eight parasite species were recorded from 504 yellow perch (*Perca flavescens*) collected from Dauphin Lake and Beaufort Lake in Manitoba, and Lake Winnebago, Green Bay, and Lake Michigan in Wisconsin. Four parasite species, *Diplostomum* spp., *Urocleidus adspectus* Beverley-Burton, 1984, *Proteocephalus pearsei*, and *Raphidascaris acus* (Bloch, 1779) occurred in all localities. Infracommunities and component communities were low in richness. Dauphin Lake and Beaufort Lake samples had the richest parasite communities, while Green Bay and Lake Michigan samples had the least rich parasite communities. The effect of host size and age on parasite community structure was equivocal. A positive association between *Proteocephalus pearsei* and *Bothriocephalus cuspidatus* and more multi-species infracommunities than expected provided evidence of non-random associations in the Manitoba samples while Wisconsin infracommunities were random associations. Significant infracommunity nestedness in all samples indicated non-random community organization and structure. Parasite faunas were richer in samples with complex invertebrate communities but not in samples with complex fish

communities. The trophic status of the aquatic system indirectly affected the parasite communities by limiting the variety of potential intermediate hosts. Predictions regarding relationships between parasite community composition and lake trophic status were not supported. I show that predictable patterns at the fine scale local level of the parasite infracommunity and component communities of perch are best explained by a rich invertebrate community upon which the host feeds.

INTRODUCTION

Describing and explaining patterns of community structure are two of the central themes of ecology but studies of parasite communities, despite advantages, have received little attention outside the discipline of parasitology (Poulin, 1995; Sousa, 1994). Parasites of freshwater fishes have been used as models to develop hypotheses regarding parasite community structure (Wisniewski, 1958; Dogiel, et al. 1958; Esch, et al. 1990; Kennedy, 1990). Parasite communities in freshwater fish are generally considered to be isolationist, random associations between few, non-interacting, species leading Kennedy (1990) to suggest that they are the result of stochastic processes. In the previous chapter it was shown that, at a continental (broad) scale, the species composition of yellow perch *(Perca flavescens)* parasite communities from North America has a predictable as well as a stochastic component (Carney and Dick, 1999). It was also acknowledged in the previous chapter that different results may obtain at smaller, more restricted, spatial scales. Defining and quantifying factors that influence fish parasite communities at the local (fine) scale are equally important in determining the effect of scale on parasite infra- and component communities and processes, and to ensure that

predictability in fish parasite communities is considered. Yellow perch is an ideal fish species to study factors affecting parasite communities because they have only one specific parasite (the gill monogenean *Urocleidus adspectus* [Cone and Burt, 1982]), which allows separation of ecological variables from those related to host specificity. Furthermore, perch parasites are regularly reported in general surveys of fish parasites (e. g. Bangham, 1944; Bangham and Hunter, 1939; Dechtiar, 1972a, b; Dechtiar et al., 1989; Fischthal, 1950; Pearse, 1924). This well documented parasite community, plus the well known biology of perch, makes it an ideal model to study all aspects of parasite transmission and distribution.

Biotic factors such as host feeding rates, vagility, and physiology have been used to explain richness in fish parasite assemblages (Kennedy et al., 1986) and to describe a model for salmonid and cyprinid parasite communities (Chubb, 1970). Host attributes such as size, age, sex, feeding guild, and phylogeny are also considered important in determining parasite richness (Aho and Bush, 1993). Both phylogenetic effects relating to host specificity, and feeding habits, were important for

structuring helminth communities in sturgeons (Choudhury and Dick, 1998).

By contrast, Wisniewski (1958) emphasized the importance of abiotic factors including host geographic range and lake trophic status on parasite species. Kennedy (1978) found that parasites of brown trout from larger lakes had more parasite species and Price and Clancy (1983) reported that fish hosts with larger distributions in the British Isles had more parasite species, although Guegan and Kennedy (1993) reinterpreted these data and argued that time since colonization was more important than host distribution. Esch (1971) emphasized that lake trophic status and increased interactions between the aquatic community and avian or mammalian species could explain differences between fish parasite communities from oligotrophic and eutrophic lakes. Esch et al. (1988) concluded that the increased number of parasites of birds and mammals in fish from eutrophic systems was due to parasites of birds and mammals having greater colonizing abilities. Hypotheses have been developed from these studies to predict that in an eutrophic system, the parasite community of fishes will be dominated by parasites of birds or mammals while the opposite will be true in an oligotrophic system.

Despite these efforts, general explanations for patterns in richness, structure and associations in parasite communities of freshwater fishes have been elusive (Aho and Bush, 1993). Perhaps this relates to insufficient emphasis being placed on the interaction between host biology and parasite transmission, especially since host feeding habits can contribute to parasite community structure. For example, helminths found as adults in the gut are most often acquired in the food of the host. The consumption of specific food items has been used to predict parasite patterns in component communities and the presence of parasites can provide insights into host feeding biology (Kennedy et al., 1992; Choudhury et al., 1996; Choudhury and Dick, 1998).

Numerous methods have been used to describe parasite community pattern, including descriptions of richness, prevalence and intensity, analytical procedures such as measurements of dominance, diversity, similarity, and chi-square analyses for species co-occurrence. Tests to explain patterns of community structure are well established in the ecological literature but infrequently used to analyze parasite communities. One of these, nestedness, was initially proposed to explain patterns of species occurrence on archipelagos. Several methods of

calculating nestedness have been proposed (Atmar and Patterson, 1993, 1995; Cutler, 1991; Patterson and Atmar, 1986; Wright and Reeves, 1992). Statistically significant nestedness appears to be a common attribute of species assemblages across taxa (Wright et al., 1998) including parasites (Guegan and Hugueny, 1994; Poulin, 1996).

The purpose of this chapter is to describe the parasite communities of yellow perch, to determine patterns of association, and to assess factors structuring these parasite communities. The parasite communities are examined, at the fine scales of infracommunities and local component communities, to determine if (1) they are stochastic assemblages (Kennedy, 1990) or have predictable components, and, (2) the parasite species are isolationist species (Holmes and Price, 1986) or if there is evidence of interactions among them. The effects of biotic (host attributes such as size, age, sex, feeding and fish community complexity) and abiotic (lake size and trophic status) factors on the parasite community of yellow perch are also evaluated.

MATERIALS AND METHODS

Perch from Dauphin Lake were collected by standard gang gill nets and trap nets set near shore. Fish were collected from early May through July in 1992 and 1993. Fish from Beaufort Lake were collected by standard gang gill nets and trap nets set in 1992 during May and June. Samples from Wisconsin were collected by trawl in August from Lake Winnebago and southern Green Bay, and in June from Lake Michigan offshore of Milwaukee.

All perch were frozen following capture. Fish were thawed, weighed to the nearest 0.1 g and measured (fork length) to the nearest mm. Liver and spleen were weighed prior to examination. The operculum was used to age the fish (Le Cren, 1947). Fish were completely necropsied; all visceral organs, eyes, gills, fins skin and flesh were examined. Livers and spleens were examined using a trichinoscope. Flesh was examined by making transverse slices across the musculature and examining the exposed surfaces.

Digeneans and cestodes were fixed in AFA, stained either in aceto-carmine or haematoxylin, cleared in xylene and mounted in Canada Balsam. Nematodes were fixed in hot 70% EtOH and cleared in glycerine

for examination as wet mounts. Identifications were made initially using Hoffman (1967), Schell (1985), and Anderson (1992) and confirmed by reference to the primary literature.

Prevalence, abundance and mean intensity was calculated for each parasite species following the definitions of Margolis et al. (1982). Values are reported as mean $\pm$ standard deviation. Infracommunity refers to the parasite community found in a host individual (Bush and Holmes, 1986a; Bush et al., 1997), whereas component community refers to the parasite community found in all hosts of a single species from a particular lake (Holmes and Price, 1986; Bush et al., 1997). Richness refers to the number of species, mean species richness refers to the mean number of parasite species per host (see Appendix 1 for discussion of richness and diversity measures). Proportional abundance is defined here as the proportion of all parasite individuals represented by a single species. Host specificity is defined here as a parasite that reproduces only in one host species. I use the term predictability to mean associations that occur with a frequency greater than 50%. The term sample refers to a collection of hosts from a particular location and year; the component community is all parasites in a sample. Samples from Dauphin and Beaufort Lakes

collectively will be referred to as Manitoba samples and those from Lake Winnebago, Green Bay and Lake Michigan collectively will be referred to as Wisconsin samples. Allogenic species are those parasites which mature in piscivorous birds (Esch et al., 1988).

A jackknife estimate of species richness in each sample was calculated using the program RICHNESS written by Krebs (1989) and a bootstrap estimate of richness was calculated using the program Species Diversity and Richness 2.1 (Pisces, 1998). Quantitative similarity between samples was calculated using the program SIMILAR written by Krebs (1989) (see Appendix 1 for discussion of similarity measures). Mann-Whitney *U* statistic was calculated to test if there was a difference between sexes on infection intensities, abundances or richness. Multiple regressions were calculated to test if host size (length), age or sex had an effect on infection intensities or richness. Correlations between lake size and species richness and mean intensity were calculated for all parasites and enteric species only. Size at age between sexes was compared within each sample using Student's t-test. Statistical tests were performed using Statview 4.0 computer software (Abacus Concepts, 1992). Results were considered to be statistically significant when $p \leq 0.05$.

Chi-square tests determined if enteric species were randomly associated among host individuals in a sample. Expected values were generated using prevalences of each species within each sample. The number of observed infections was compared to the expected number of uninfected fish, fish with single species infracommunities and fish with multi-species infracommunities, in order. Remaining groups were pooled when subdividing the remaining categories did not provide expected values greater than one.

Nestedness of the parasite infracommunities within samples was calculated using the nestedness calculator described by Atmar and Peterson (1993, 1995). For each sample a presence-absence matrix of parasite species in each infracommunity was constructed. Each matrix was reordered so as to maximize species presence in the upper left corner. The reordered, or packed, matrix was then compared to a maximally nested matrix having the same proportion of species presence. In this way, the unexpected presence or absence of a species in the observed matrix could be identified. For each observed matrix, a value T was calculated where 0 represents a perfectly nested matrix and 100 represents a completely random matrix. Significance of the observed T

value was determined by simulation of randomly generated matrices. For each sample, the T value of the observed matrix was compared to the distribution of T values generated by 500 runs of randomized matrices.

Stomach contents were recovered, initially identified to order, and stored in 70% EtOH for subsequent identification. Food items were reported as frequency of occurrence and grouped according to transmission route; fish, pelagic zooplankton, benthic Coleoptera and Hymenoptera, benthic Amphipoda, larval Trichoptera, Ephemeroptera, Odonata and Chironomidae, clams, leeches, fish roe and seeds. Parasites were categorized as being transmitted by cercarial penetration, direct infection, and food items, (pelagic, benthic and fish).

Comparisons among samples in the number of allogenic species and dominance by allogenic species were made to assess the hypothesis of Esch (1971) and Esch et al. (1988) regarding the role of lake trophic status as a factor affecting the composition of the parasite community.

Dauphin Lake

Located in southwestern Manitoba (51°17'N, 99° 48'W) (Figure 3), Dauphin Lake, is 42 km long, 20 km wide, has a surface area of approximately 520 km^2, mean depth of 2.1 m and a maximum depth of

3.5m (Babaluk and Friesen, 1990). There is a single outflow draining to the north (Oshoway and Penner, 1982). The lake bottom is fine silt or mud, and the shoreline is sand, gravel and boulder beaches with some marshy areas. Although often considered to be eutrophic because of its high productivity and turbidity, Dauphin Lake is well mixed, has O_2 levels at or near saturation levels, and chlorophyll levels similar to mesotrophic lakes. Much of the turbidity is a consequence of resuspended particulate sediment stirred up from the bottom (Babaluk and Friesen, 1990). The rich invertebrate biota is consistent with a mesotrophic lake (Friesen and Mathias, 1990) and it harbours approximately 27 species of fish including esocids, cyprinids, percids and eutrophic-intolerant coregonids (Szalai, 1989; Szalai et al., 1992; Babaluk et al., 1992). Dominant fish predators include pike and walleye.

Beaufort Lake

Located in southwestern Manitoba (50° 30'N, 100° 10'W) (Figure 3), Beaufort Lake (Lake 611, Aquaculture Experimental Lakes, Erickson-Elphinstone Area) is a crescent-shaped prairie-pothole seepage lake with no inflow or outflow streams (Barica et al., 1978; Sunde and Barica, 1975). The surface area is approximately 1.5 km^2. The depth is not

known, but personal experience and the fact that it does not winterkill, suggests it is deeper than 3 m. The steep shoreline has many areas of emergent vegetation and a rich community of rooted submerged vegetation. There are no data to assess the trophic status of this lake but our observations indicate a meso- to eutrophic lake. There also are no data on the fish fauna but only yellow perch and northern pike (*Esox lucius* L.) were caught in standard gang gill nets and only yellow perch and brook sticklebacks (*Culaea inconstans* [Kirtland, 1841]) were recovered from the trap nets.

Lake Winnebago

Located in east-central Wisconsin, Lake Winnebago (44°00'N, 88°25'W) (Figure 3) is approximately 45 km long, 16 km wide, has a surface area of approximately 557 km^2, mean depth of 4.7m and maximum depth of 6.4m (Wirth, 1959). Lake Winnebago is highly eutrophic due to human activity (Wirth, 1959). The lake bottom is soft mud and silt with sand/clay or gravel/rubble shorelines. There is little emergent vegetation on the eastern shoreline while on the west there is dense vegetation along sheltered shores (Becker, 1964). The invertebrate fauna is dominated by species tolerant of eutrophication, especially

chironomid larvae, oligochaetes, copepods, and cladocerans (Wirth, 1959). Invertebrates sensitive to eutrophication, such as ephemeroptera, trichoptera, and odonata are absent or very rare. There are approximately 37 fish species reported from this lake with freshwater drum, white bass and yellow perch being the most abundant (Becker, 1964). Dominant predators include white bass, walleye, and pike.

Green Bay

Extending from the northwest portion of Lake Michigan, Green Bay (44°35'N, 87°55'W) (Figure 3) is 190 km long, has a mean width of 37 km and a total area of approximately 4116 km^2 (Balch et al., 1956; Sager and Richman, 1991). Green Bay is shallowest in the south (2-3m), where anthropogenic input from the Fox River provides a high nutrient load contributing significantly to the hypereutrophic nature of the southern bay (Howmiller and Beeton, 1971; Sager and Richman, 1991). Fish were sampled from the southern portion of Green Bay. In this portion of the bay, the macrobenthic invertebrates are primarily chironomid larvae and oligochaetes while species such as mayfly larvae and odonata are absent (Gannon, 1974). The pelagic zooplankton are primarily copepods and cladocerans. Alewife (*Alosa pseudoharengus*

[Wilson, 1811]), bloater (*Coregonus hoyi* [Gill, 1972]), and rainbow smelt (*Osmerus mordax* [Mitchill, 1814]) are the predominant forage fish and artificially stocked and maintained salmonids are the dominant piscivores. Yellow perch were a dominant fish species, but in recent years their populations have declined (Wells, 1977).

Lake Michigan

Lake Michigan (43°00'N, 87°30'W) (Figure 3), is 494 km in length, has a maximum width of 190 km, and an approximate surface area of 58,000 km^2. Mean depth is 84m with a maximum of 281m. This lake is oligotrophic (Lehman, 1988). The fish fauna has changed in the last 50 years due to invasions by fish species such as alewife and rainbow smelt (Wells, 1977) and the stocking of salmonid species (Stewart and Ibarra, 1991). A wide range of invertebrate fauna are present and their abundances reflect local conditions. Yellow perch were sampled in the southwestern portion of the lake, offshore from Milwaukee.

RESULTS

Parasite species

Twenty-eight species of parasites were recovered from yellow perch in the 6 samples (Table 4), of which 12 were enteric species and 5 were ectoparasite species. Eleven larval species were present in the component communities of which 6 were allogenic. Species compositions were identical between the 1992 and 1993 Dauphin samples and quantitative similarity was also high between these two samples (Table 5). Quantitative similarity was lowest between the Beaufort and Green Bay samples and Beaufort and Lake Michigan (Table 5). Species present in all samples were metacercariae of the digenean *Diplostomum* spp., adults of the monogenean *Urocleidus adspectus*, the cestode *Proteocephalus pearsei*, and larvae of the nematode *Raphidascaris acus* (Table 4). The only parasite specific for yellow perch recovered in this study was *Urocleidus adspectus* (Cone and Burt, 1982). Jackknife and bootstrap estimates of species richness were higher than observed for all samples (Table 6). The variance in the jackknife estimates indicated the number of species in Lake Winnebago was not different than in Beaufort Lake samples (Table 6) which was inconsistent with our observations.

When all parasite species were considered mean species richness, intensities and abundances were highest in the Dauphin Lake sample and lowest in the Lake Winnebago sample (Table 7). Beaufort Lake had the second highest number of parasite species despite being the smallest of the systems studied. There was no significant correlation between total richness, enteric richness or mean intensity and lake size or fish community richness.

Enteric species

Component community enteric species richness ranged from 6 in the Dauphin Lake samples to 4 in the Beaufort and Green Bay samples (Table 7). Four enteric species each were unique to single samples (Table 4). Enteric infracommunity mean richness ranged from 2.1 in the 1992 Dauphin Lake sample to 1.1 in the Green Bay and Lake Winnebago samples (Table 7). Abundance values ranged from 38.5 in the 1992 Dauphin sample to 0.1 in the Green Bay sample. Prevalence of enteric parasites was highest in the Lake Michigan sample and lowest in Lake Winnebago and Green Bay samples (Table 7).

Allogenic species

Allogenic richness ranged from 5 species in the Beaufort sample to 2 species in Lake Michigan and Green Bay samples (Table 7). Allogenic infracommunity mean richness ranged from 1.4 in the 1992 Dauphin sample to 1 in the Green Bay sample. Proportional abundance of allogenic species ranged from 69% of all individuals in the Winnebago sample (Table 7) to 4% in the Green Bay sample. Oligotrophic Lake Michigan had the second highest proportional abundance of allogenic species and the highest intensity of infection by allogenic species. Prevalence of allogenic parasites was highest in the 1992 Dauphin Lake sample and lowest in the Green Bay sample (Table 7).

Host attributes

Although host size and age were generally quite similar among samples, some differences were apparent. Yellow perch in the Lake Michigan sample were, on average, larger and older than hosts in the other samples (Table 8), Green Bay perch on average were the smallest and youngest and the 1992 Dauphin sample had the greatest range in size and age (Table 8). Young of the year (YOY) fish were collected only in the 1992 Dauphin sample. Only in the Michigan sample was there an absence of fish younger than 3+. Male fish 5+ or older were uncommon

or absent, and males 6+ or older were present only in the Lake Michigan sample.

Four separate year classes had significant differences in size at age between males and females. The single age 2+ male was significantly larger than females in the 1992 Dauphin sample. Males were significantly smaller than females in age classes 3+ and 4+ from the Beaufort sample, and in age class 4+ from the Green Bay sample. There was no significant difference in size at age between male and female hosts in all other age classes.

Infection vs. host size

The effect of host size, age and sex varied among samples and differed among parasite types (Tables 9, 10, 11), although even when all variables were combined the total predictive effect was generally low. If all parasite species were combined, host size had a significant effect on richness in both Dauphin samples the Beaufort sample and the Lake Michigan sample (Table 9) and on intensity in the 1992 Dauphin sample and the Beaufort and Green Bay samples. Enteric species richness, abundance and intensity correlated with host size in the 1992 Dauphin sample, but not the 1993 Dauphin sample. If only enteric species were

considered, host size had an effect only on species richness in the Beaufort sample. Host size had an effect on allogenic species intensity in the 1992 Dauphin and Beaufort samples. correlated positively with host size in all 3 Manitoba samples. Ectoparasite richness varied significantly with increased host size in the 1992 Dauphin and Beaufort samples and ectoparasite intensity varied with size only in the 1992 Dauphin sample (Table 9).

Infection vs. age

All-species richness varied significantly with host age in the Beaufort and Lake Michigan samples (Table 10) and all-species intensity varied significantly with age in the 1993 Dauphin and Lake Michigan samples. Only the Beaufort sample showed significant variation between host age and allogenic species richness (Table 10). If only ectoparasites are considered the effect of age was significant only for richness and intensity in the 1992 Dauphin sample and intensity only in the 1993 Dauphin sample (Table 10).

Infection vs. sex

All-species intensity ($p = 0.02$) and abundance ($p = 0.02$) was higher in males than females in the 1993 Dauphin sample, while enteric

species intensity ($p = 0.05$) and abundance ($p = 0.02$) and allogenic species intensity ($p = 0.01$) and abundance ($p = 0.03$) was greater in males in the 1992 Dauphin sample. There was no statistical difference observed between the sexes in any of the other samples. Sex contributed parasitism only in the Dauphin samples. The 1992 sample showed an effect of sex on all-species richness and intensity, allogenic intensity and ectoparasite richness and intensity. The 1993 sample showed an effect only on ectoparasite richness.

Species associations

Dauphin and Beaufort Lakes were the only samples with infracommunities having significant departures from random species association (Tables 11-16). There were 2 sources of high chi-square values in the Dauphin samples. In the 1992 sample, there were more infracommunities comprised of 4 or more species and there were fewer uninfected fish than expected (Table 12). All infracommunities of 4 or more species included the cestodes *Proteocephalus pearsei*, *Bothriocephalus cuspidatus* and the digenean *Crepidostomum cooperi*. The absence of *B. cuspidatus* single species infections in this sample contributed also to the chi-square significance. In the 1993 Dauphin

sample high chi-square values also resulted from a greater than expected number of infracommunities with 4 or more species (Table 13). The cestodes *P. pearsei*, *B. cuspidatus* and the digenean *C. cooperi* were present in 4 of those infracommunities. A single perch had an infracommunity comprised solely of *B. cuspidatus*.

In the Beaufort sample more infracommunities than expected had more than two species and fewer infracommunities than expected had only *B. cuspidatus* (Table 14). The cestodes *Proteocephalus pearsei*, *Bothriocephalus cuspidatus* and the digenean *Bunodera luciopercae* were present in all of the infracommunities with more than two species.

The Wisconsin samples did not have parasite communities that departed significantly from random based on species prevalence (Tables 14-16). Although *Bothriocephalus cuspidatus* was present in the component community of Lake Winnebago (Table 4), it was not observed as a single species infracommunity (Table 15).

Nestedness

There was significantly more nestedness than expected by chance in the infracommunities from each sample (Table 18). Matrix fill ranged from 9.9% in the Winnebago sample to 34.4% in the Lake Michigan

sample. T values ranged from 6 in Beaufort sample to 22 in the 1992 Dauphin sample. The 1993 Dauphin sample was less filled and more nested than was the 1992 Dauphin sample (Table 18).

Stomach contents

Different food items dominated the stomach contents in each sample (Table 19). Hosts in the Beaufort sample had the greatest number of food items (10) whereas hosts in the Lake Michigan sample had the fewest (2) (Table 19). Fish and cladocerans were most common in the Dauphin samples whereas fish and amphipods dominated in the Beaufort sample. Cladocerans were recovered most frequently in the Green Bay sample and in the Winnebago sample cladocerans and chironomids dominated. Fish was the dominant food item in the Lake Michigan sample but the majority of perch in this sample had empty stomachs.

DISCUSSION

The previous chapter showed that, despite the absence of enteric host-specific parasites, there was a predictable component to the parasites associated with *Perca fluviatilis* in Eurasia and *P. flavescens* in North America at the broad continental scale (Carney and Dick, 1999). If there are comparable recognizable structure and predictability, at the fine or local scale, for infra- and component communities then it is here that factors affecting patterns in parasite communities can be best quantified and processes leading to community structure assessed. Recognizing patterns within and among the different parasite communities is the first step in assessing the contributions of biotic and abiotic variables.

Pattern

Whether parasite communities have predictable patterns is a central question in parasite community ecology. One of the commonly sought patterns is taxonomic. Taxonomic predictability in my data was indicated by the presence in all samples of *Urocleidus adspectus*, *Proteocephalus pearsei*, *Raphidascaris acus*, and *Diplostomum* spp. *Proteocephalus pearsei* has been identified in Chapter 1 as belonging to a suite of 4 enteric parasites predictably associated with yellow perch at the broad

continental scale (Carney and Dick, 1999). Of the remaining 3 enteric species, I found that *B. cuspidatus* was present in 4 of the samples, *C. cooperi* was present in 3, and *Dichelyne cotylophora* was present in a single sample. This supports the contention that some or all of these species will occur in the parasite component community of yellow perch. *Urocleidus adspectus* was present in all my samples and is specific to yellow perch (Cone and Burt 1982). This parasite is a contributor to community predictability and that it should be added to the suite of predictable parasites for component communities of yellow perch in North America. Although there is taxonomic similarity among samples there is not the same degree of similarity in their species proportional abundances. For example, Beaufort Lake and Lake Michigan share 7 species but have a quantitative similarity of 0.09. This difference is because the shared species have low abundance in either or both of these samples.

Host attributes

Host attributes including size, age and sex are frequently considered important contributors to parasite infracommunity community structure (Dogiel, 1958; Esch et al., 1975; Humphrey et al., 1978;

Kennedy et al., 1986; Zelmer and Arai, 1998). However, it is difficult to isolate the effect of host size on parasitism from the effect of host age since size and age are often highly correlated. Predictions are that long-lived persistent parasites (allogenic species) will accumulate with host age while short-lived parasites (enteric species) acquired in food will accumulate with host size (Zelmer and Arai, 1998). As a general trend in my samples larger fish were older, but the pattern was not consistent regarding size dimorphism between sexes within each age class and there was considerable size variation within, and overlap between, year classes and is consistent with other reports (Le Cren, 1947; Noble, 1975; Craig, 1987; Mills et al., 1989; Boisclair and Leggett, 1989; Steggs and Otis, 1996). However, some differences between samples/locations were noted in my data. In the 1992 and 1993 Dauphin sampless richness varied with size but not age. Higher enteric infections varied with size but not age in the Beaufort sample which is consistent with the predictions of Zelmer and Arai (1998). However, this does not extend to the Dauphin samples where there was no significance between size and enteric infection.

Only in the Beaufort sampple was there a significant effect of age on accumulation of long-lived species. Increased allogenic intensity

varied with size but not age in both Dauphin samples and the Lake Michigan sample. Absence of an effect of host age or size on parasitism in the Lake sample may be explained by the large numbers of uninfected fish. Clearly, the predictions of Zelmer and Arai (1998) do not apply to all samples or systems and at this time I am unable to generalize about the effect of size and age on different aspects of parasite infections in yellow perch. Perhaps these differences between my data and those of Zelmer and Arai (1998) relate to the nature of the samples (number and time of collection, size/age and sex ratio of host) and/or some host trait as yet undefined.

There has been little support for host sex as a factor influencing parasite communities of fishes. Studies on parasites of bowfin (*Amia calva*) (Aho et al., 1991), spot (*Leiostomus xanthurus*) and croaker (*Micropogonias undulatus*) (Thoney, 1993), and lake sturgeon (*Acipenser fulvescens*) (Choudhury and Dick, 1993), reported no difference between sexes in parasite infections although Lawrence (1970) detected slight correlations with host sex by some parasites of suckers (*Catostomus commersoni*). In my samples host sex had a significant effect on parasitism only in the Dauphin samples. Male fish in the 1992 Dauphin

sample had significantly higher richness and intensities and of all-species and ectoparasites, and higher intensities of allogenic species intensity, than female fish. Sex had an effect on ectoparasite richness in the 1993 Dauphin sample.

Random vs. predictable communities

If there is evidence of community structure in yellow perch parasite communities, we should see repeated patterns in the infracommunities within samples and in component communities among samples. My samples from diverse sites provided the opportunity to observe these repeated patterns, but the host attributes need to be similar. There was a remarkable degree of similarity between the Dauphin Lake samples. Size and age of the yellow perch were similar, parasite species composition was identical and correlations with different aspects of the parasite communities were almost identical. Although the parasite species richness and composition were identical, proportional representation by each parasite species was different between the two years. This is not surprising since it is known that parasite populations from the same location vary amongst years (Kennedy, 1990). Nonetheless, the quantitative similarity between these 2 samples was quite high (0.88).

The taxonomic consistency between these samples extended to species associations within the infracommunities. The Dauphin Lake samples had more infracommunities with 4 or more species than expected by chance and 3 of these (*Proteocephalus pearsei*, *Bothriocephalus cuspidatus, Crepidostomum cooperi)* were always present. The Beaufort sample had a greater than expected number of infracommunities with *B. cuspidatus*, *P. pearsei*, and *Bunodera luciopercae*. These associations may relate to transmission dynamics and feeding habits since *Bothriocephalus cuspidatus* and *P. pearsei* use copepods as intermediate hosts (Bangham, 1925), *B. luciopercae* use cladocerans (Cannon, 1971) and *C. cooperi* use mayfly larvae (Choquette, 1954). Bush et al. (1993) and Dick (unpublished data) found single intermediate host individuals infected with two or more different parasite species are capable of transmitting an instant infracommunity to a definitive host. Similarly, since a particular food source, e.g. pelagic zooplankton in the Beaufort sample, could host intermediate stages of more than one species of parasite, then multi-species infections may be a direct consequence of this food. This provides a process for forming richer infracommunities and for species to be in association more frequently than expected by chance.

By contrast, parasite species did not depart from random co-occurrence in the Wisconsin samples. In these samples the observed patterns of parasite species association were remarkably close to those expected based on species prevalence, and relative to the Manitoba samples, were depauperate and random communities. The samples from Wisconsin are affected by anthropogenic factors and results were the most consistent with predictions by Kennedy (1990) that freshwater fish parasite communities are stochastic communities. By comparison, the samples from Dauphin and Beaufort lakes are less affected by humans, as evidenced by a more diverse parasite-transmitting invertebrate community and being from less eutrophic lakes. Despite having low richness, the non-random associations among some parasite species in the infracommunities and the taxonomic similarity observed among component communities in the Manitoba samples indicates that not all perch parasite populations were random at a fine or local scale.

In my samples single species infracommunities occurred at a frequency that was consistent with what would be predicted based on prevalence. The exception is *B. cuspidatus* which was predicted to occur as a single species infection in a total of 13 infracommunities but was

observed only once in the 4 samples in which it occurs and was always present with *P. pearsei* in the other infracommunities. This absence could relate to concurrent transmission through consumption of the same copepod intermediate host infected with *P. pearsei*, but this should result in fewer than expected *P. pearsei* single species infections, which is not the case. Perhaps this positive interaction between these species results in a greater chance of establishment of *B. cuspidatus* in the presence of *P. pearsei*. It could occur either in the copepod or perch hosts and provides evidence that communities considered to be depauperate can be interactive.

Community Structure

The search for structure in parasite communities has been a central issue in parasite community ecology (Esch et al., 1990). Parasite communities of freshwater fishes have been used as model systems to develop hypotheses to describe and assess parasite community structure. Concepts such as infra- and component communities are unique to parasite communities, while others, such as the concept of community nestedness are adopted from studies of communities of free living organisms. Nestedness explains patterns in species presence on

archipelagos and was first applied to parasite communities by Guegan and Hugueny (1994). Communities are said to be nested if species present in species-poor communities are successive subsets of those present in species-rich communities (Atmar and Patterson, 1993).

Infracommunity in all samples were significantly nested despite having few taxa, relatively empty matrices, different numbers of parasite species and coming from trophically different systems. The apparent ubiquity of nestedness suggests a common pattern for parasite infracommunities and that infracommunities are not merely communities randomly drawn from the species available in the component community. Even at the fine or local scale of the infracommunity, repeated patterns of community structure are present in perch, which primarily has nonhost specific parasites. Processes suggested for producing nestedness include the addition of species in a consistent order from a common pool, differential dispersal abilities, differential susceptibility to local extinction, nestedness of habitat, distance of islands from a source of colonizers, species range requirements, and passive sampling (Wright and Reeves, 1992; Wright et al., 1998). Differential susceptibility to infection may be added to this list when considering parasite communities.

Although some of my samples indicated differences in host suitability based on age, size or sex there was no consistent pattern across all samples and this may not be the explanation for the nestedness observed in all samples. More likely factors are passive sampling, sequential colonizing ability, or extinction differences. The passive sampling hypothesis predicts that common species will be in many hosts and rare species will be in few hosts and that a nested subset pattern will result based only on probability. In the absence of information on population sizes of the infective stages I cannot eliminate passive sampling as a possible explanation for the nestedness I see in my data. Sequential colonization is possible since different parasite taxa are infective at different times of the year. Differential extinction can also occur since some parasites have seasonal life cycles while others are comparatively long lived. Nonetheless, since parasite infracommunities are assembled by comparatively few processes, they provide a promising model for determining the processes responsible for nestedness of communities.

Diet and Feeding Habits

Diet is considered a key factor contributing to parasite community structure (Dogiel, 1958; Kennedy et al., 1986; Bush et al., 1993;

Choudhury et al., 1996; Choudhury and Dick, 1998) and combining stomach contents and parasite data can provide a more comprehensive picture of host feeding habits and dietary preferences. Yellow perch are considered to be generalist omnivores feeding opportunistically on what is available (Thorpe, 1977; Craig, 1987), but in my samples the importance of diet in structuring the yellow perch parasite communities varies among samples and depends on whether richness or abundance is considered.

Dietary items varied among perch populations with the most diverse species list being found in Beaufort Lake samples. It should be noted that dietary items remain in the gut for about 24 hours in perch (Persson, 1979; 1981) while parasites reflect prior feeding and my fish samples clearly reflect this (see below) as some food items were absent but there was extensive parasitism. For example, Dauphin Lake perch in our sample fed primarily on minnows, but 8 parasite species were transmitted by copepods, amphipods or insect larvae. While benthic organisms dominated the stomach contents of the Beaufort perch samples, and benthic transmitted parasites *Bunodera*, *Raphidascaris* and

Spinitectus were present, high abundances of *Bothriocephalus* and *Proteocephalus* indicated pelagic planktivore feeding as well.

The most common food items in Lake Winnebago perch samples were cladocera and chironomid larvae which is consistent with earlier reports of chironomid larvae being the dominant macrobenthic organism (Wirth, 1959). Due to the hypereutrophic status of Lake Winnebago insect species such as larval Ephemeroptera, Trichoptera or Odonates, are either absent from Lake Winnebago, or extremely rare (Priegel, 1963) and were not recorded in the stomach contents. This absence of insect larvae, known to transmit perch enteric parasites, limits the number of parasite species. The presence of *Crepidostomum cooperi* in 2 perch may result from infections acquired outside of Lake Winnebago as perch are known to migrate to the Fox and Wolf Rivers (Weber and Les, 1982) which support mayfly larvae, the intermediate host for this parasite (Choquette, 1954). A similar observation was made on the distribution of parasites in lake sturgeon from the same system (Choudhury et al., 1996). The presence of *Cyathocephalus truncatus* indicated amphipods in the diet, an item not recorded in the stomach contents. The rich chironomid

fauna and large fish-eating walleye population may account for the absence of fish in the diet in Lake Winnebago perch.

Parasites that use intermediate hosts intolerant of eutrophic conditions were absent in the Green Bay samples. For example, the zooplankton is dominated by copepods and cladocerans, and benthic fauna is mostly tubificid oligochaetes and chironomid larvae while insect larvae such as mayflies are absent (Balch et al., 1956; Gannon, 1974). Stomach contents comprising mostly chironomid larvae were consistent with these reports. The presence of *Eustrongylides* sp. transmitted through oligochaetes (Measures, 1987), *R. acus* through chironomid larvae (Smith, 1984), and *P. pearsei* and *Camallanus lacustris* both transmitted through copepods (Hoffman, 1967), provide additional information on the feeding habits of perch in this system.

It is difficult to assess directly the feeding habits of perch in the Lake Michigan sample since 76% of the perch had no food in their stomachs, and of those with food, 7 had fish and 2 had larval insect remains. High prevalence and abundance of *Echinorhynchus salmonis* and *P. pearsei,* respectively, indicated that amphipods and copepods were important food items. Species such as *Spinitectus gracilis* and 3

acanthocephalan species also indicated the importance of invertebrates in their diet. This is a good example of how parasite data contributes to our knowledge of perch food habits.

Diet and Parasite Community Structure

Hosts with broad diets are predicted to have more parasites than those with narrow dietary preferences (Dogiel, 1958; Kennedy et al., 1986). If this hypothesis is true then it follows that host species with a variety of available food items will likely have more parasites than the same host exposed to a restricted set of potential food items. Evidence from stomach contents and parasite infections indicated that perch in all five systems were feeding on benthic organisms, pelagic organisms and, with the exception of the Lake Winnebago sample, other fish. In the broadest sense their feeding habits were essentially the same and the presence of specific food items in the waterbody affected the presence of enteric parasites. Dauphin and Beaufort Lakes have a more diverse invertebrate fauna with a potential to transmit a greater variety of parasites (Cobb and Flanagan, 1987; Friesen and Mathias, 1990). The added parasite richness in Dauphin Lake and Beaufort Lake correlated with a more diverse invertebrate community, much of which is absent in

the two Wisconsin systems. Since larval Ephemeroptera and Odonata were absent from Lake Winnebago and Green Bay, parasites transmitted by these hosts were also absent. The simplified invertebrate fauna in the Wisconsin systems appears to be the result of the trophic status of the lake.

Food type contributed more to parasite abundance and less to species richness in the Manitoba samples. Food items in the Dauphin Lake samples transmitted greater than 80% of parasite total abundance but 50% of species richness. Transmission through food items also contributed most of the parasite abundance in the Beaufort Lake sample, but about half of the total richness. By contrast, food was a greater source of parasite richness while non-food sources contributed more to abundance in the Wisconsin samples. In the Green Bay sample, food items transmitted the majority of parasite species but these parasites occurred infrequently and in low numbers, and contributed relatively little to abundance. In the Lake Michigan sample, the majority of parasite richness was due to transmission through food items, while total abundance resulted primarily from cercariae. These patterns highlight the differential contribution of food items to patterns of parasitism.

Fish Community

Chubb (1970) emphasized the role of the fish community and proposed that salmonids and their parasites would dominate in oligotrophic systems, cyprinids and their parasites would dominate in eutrophic systems whereas mesotrophic systems would have the richest parasite fauna because they had the richest fish fauna. Complexity of the fish community had little apparent effect on parasite species richness in my samples. Beaufort Lake and Dauphin Lake with the two simplest fish faunas, had the greatest number of parasite species. However, these were both mesotrophic systems. Perhaps Chubb (1970) is correct in suggesting that fish in mesotrophic systems have the richest parasite fauna, but this is not a necessarily a consequence of complexity of the fish community. There was no evidence from my samples that a richer fish community results in a richer parasite community in yellow perch.

Lake Size and Trophic Status

Lake size had no obvious influence on the parasite communities reported here, despite being considered an important contributor to the complexity of the parasite community in fishes (Dogiel, 1958; Kennedy, 1978). Beaufort Lake, the smallest in our samples, had the second highest

number of parasite species while the two largest systems, Green Bay and Lake Michigan, had the fewest parasite species.

Lake trophic status is considered important in determining the parasites present in fish hosts. Wisniewski (1958) proposed for eutrophic lakes that the majority of species will be parasites of piscivorous birds if all parasites are considered (i.e., the compound community). Subsequently, Wisniewski (1958) has commonly been misinterpreted as stating that in an eutrophic lake the parasites of fish will be dominated by parasites which mature in piscivorous birds. Inspection of Wisniewski's (1958) data found that the majority of parasite species in fish hosts were parasites which matured in fish, not piscivorous birds. Esch (1971) compared the parasite communities of centrarchids from oligotrophic and eutrophic lakes and predicted that allogenic species would dominate in fish hosts from eutrophic systems, and autogenic species would dominate in fish hosts from oligotrophic systems (Esch et al., 1988). Based on Esch (1971) and Esch et al. (1988), the prediction is that the Winnebago and Green Bay samples would have the greatest richness and abundance of allogenic species and the Lake Michigan samples would have the lowest richness and abundance of allogenic species. These predictions are not

supported by my data. The greatest richness of allogenic species in perch occurred in mesotrophic Beaufort Lake. Many piscivorous birds were observed foraging on Beaufort Lake and the small size of the lake and limited fish fauna may assist in concentrating allogenic species in the available fish hosts. Dauphin Lake samples, where migrating birds may provide a pulse of infective stages, had the second highest number of allogenic species. Hosts from highly eutrophic Lake Winnebago and Green Bay respectively had fewer allogenic parasite species than autogenic parasite species. The low numbers of allogenic species in the Lake Winnebago sample is worth noting given its overall similarity to Dauphin Lake. Much of the original aquatic bird habitat has been lost due to human activity (Ron Bruch, Wisconsin Fish and Wildlife, pers. comm.) and while some bird species are common on Lake Winnebago it is not as important for the staging of migratory fish-eating birds as Dauphin Lake. Hosts from oligotrophic Lake Michigan had the same number of allogenic species as eutrophic Green Bay. It is clear that the trophic status of the waterbody cannot be used to predict the allogenic richness of perch parasite communities.

Similarly, parasite abundance did not follow the predictions of Esch (1971) and Esch et al. (1988). Allogenic parasites represent the majority of abundance in the component community of perch in each of Beaufort Lake, Lake Winnebago, and Lake Michigan. These three habitats are mesotrophic, eutrophic, and oligotrophic, respectively. This is unexpected since, according to Esch (1971) and Esch et al. (1988), an oligotrophic system should be dominated by autogenic species. It is apparent that the trophic status of the waterbody cannot be used to predict the allogenic abundance of perch parasite communities.

In my study, mesotrophic systems with rich invertebrate intermediate hosts had the richest parasite infracommunities. This rich and abundant invertebrate community makes possible a rich parasite community. The absence of a rich invertebrate community in eutrophic Lake Winnebago and Green Bay resulted in depauperate parasite infracommunities and component communities. Oligotrophic Lake Michigan also has a depauperate parasite community. Pearse (1924) reported 15 species of parasites from yellow perch in Lake Michigan but Amin (1978) and Amin and Burrows (1977) found fewer parasites. My data are consistent with these more recent studies indicating the parasite

fauna has changed. These changes to the parasite fauna may be attributed to biotic changes, especially to the fish fauna, that have occurred in Lake Michigan in recent decades (Brandt et al., 1991; Morsell and Norden, 1968). It is worth noting that while the fish fauna has changed in composition, the parasite fauna in yellow perch has lost species highlighting the dependence of parasites on the whole system.

In summary, at the fine scale of the infracommunity there was evidence for non-random species associations and there was predictability in the pattern of parasite species communities in perch in some of the aquatic systems studied. This agrees with the observations in Chapter 1 (Carney and Dick, 1999) that there is predictability, at the broad continental scale, in the parasites associated with perch in North America and Eurasia. At the fine scale of local component and infracommunities, determinants of these patterns were more related to biotic factors than to abiotic influences. The fish host influences were variable within and among samples and differed with the type of parasite. In general, fish host factors had a greater influence on parasitism in mesotrophic systems. The most important determinant in structuring the parasite communities of yellow perch from the five locations in my study related to the presence

of a rich invertebrate fauna capable of transmitting parasites. This invertebrate fauna is limited by the trophic nature of the water body and, consequently, the trophic status of the water body indirectly affects the parasite community by limiting the diversity of the invertebrate community. However, for my data, lake trophic status was not a consistent predictor of dominance by allogenic species in the parasite community and contributed to stochasticity in perch parasite communities. It is clear that parasite data provides additional insights into the ecology of the host and that the parasite community is the end result of all factors in the aquatic ecosystem. Consequently, information on parasites may predict more about the host and its environment than does the host and environment predict about the parasite community.

Table 4. Infection parameters for parasite species of yellow perch (*Perca flavescens*) from Dauphin Lake and Beaufort Lake, Manitoba and Lake Winnebago, Green Bay and Lake Michigan, Wisconsin. Number of fish examined from each locality indicated by (n). Prevalence* is followed by mean intensity ± SD† with range‡ in parentheses.

Parasite	Route of Infection	Site of Infection	Dauphin Lake 1992 (n = 63)	Dauphin Lake 1993 (n = 102)	Beaufort Lake (n = 99)	Lake Winnebago (n = 95)	Green Bay (n = 107)	Lake Michigan (n = 38)
Ectoparasites								
Urocleidus adspectus	direct	gills	42.8* 5.5 ± 6.2† (1-27)‡	36.2 7.8 ± 5.3 (1-22)	19.2 4.8 ± 6.96 (1-30)	2.1 2.5 ± 0.70 (2-3)	60.7 3.7 ± 2.76 (1-13)	92.1 5.5 ± 4.50 (1-17)
Ergasilus luciopercarum	direct	gills	11.1 2.1 ± 2.0 (1-6)	13.7 3.2 ± 2.7 (1-11)	1.01 6 (6)	0	72.8 3.8 ± 2.92 (1-15)	36.8 1.7 ± 1.25 (1-5)
Anodonta sp. Glochidia	direct	gills and fins	22.2 5.2 ± 6.0 (1-24)	3.9 3.5 ± 3.1 (1-8)	2.02 3.5 ± 3.53 (1-7)	1.05 8 (8)	0	0
Lampsilis sp. Glochidia	direct	gills	6.31 1.2 ± 11.8 (1-23)	3.9 14 ± 9.0 (3-24)	0	0	0	0
Myzobdella moorei	direct	fins and body surface	33.3 2.3 ± 1.5 (1-6)	24.5 2.9 ± 1.6 (1-6)	19.2 2.4 ± 1.6 (1-7)	0	0	0
Larval Parasites								
Apophallus sp.	cercarial penetration	flesh and fins	42.8 5.8 ± 7.2 (1-32)	33.3 4.8 ± 4.2 (1-17)	8.08 6.2 ± 14.05 (1-41)	16.8 5.3 ± 6.9 (1-27)	0	78.9 27.6 ± 35.7 (1-174)

Clinostomum sp.	cercarial penetration	flesh	1 1 (1)	1.9 1.5 ± 0.7 (1-2)	3.03 11 ± 13.85 (3-27)	0	0	0
Diplostomum spp.	cercarial penetration	eye	26.9 4.2 ± 4.8 (1-15)	21.5 3.5 ± 3.5 (1-13)	77.7 12.8 ± 13.3 (1-72)	33.6 3.2 ± 2.3 (1-9)	2.8 6 ± 4.3 (1-9)	5.2 1 (1)
Neochasmus sp.	cercarial penetration	eye and flesh	33.3 2.6 ± 1.8 (1-8)	24.5 2.5 ± 1.1 (1-5)	0	0	0	0
Posthodiplostomum sp.	cercarial penetration	skin and flesh	0	0	0	2.1 12.5 ± 14.8 (2-23)	0	0
Metacercaria	cercarial penetration	encysted on intestine	0	0	11.1 3 ± 3.1 (1-11)	1.05 3 (3)	0	0
Triaenophorus nodulosus	copepod ingestion	liver	12.6 1.3 ± 1.0 (1-4)	8.8 1.2 ± 0.4 (1-2)	0	2.1 2 ± 1.41 (1-3)	0	0
Ligula intestinalis	copepod ingestion	body cavity	1.5 2 (1)	0.9 1 (1)	3.0 31.6 ± 1.15 (1-3)	0	0	0
Agamonema	unknown	intestine	0	0	0	7.3 1.8 ± 0.9 (1-3)	20.5 4 ± 5.4 (1-21)	0
Eustrongylides sp.	oligochaete ingestion	encysted on intestine	0	0	2.0 1.5 ± 0.70 (1-2)	0	7.4 2.1 ± 1.1 (1-4)	0
Raphidascaris acus	insect larvae/fish ingestion	liver and mesentery	61.9 11.2 ± 11.7 (1-40)	65.6 13.4 ± 14.3 (1-64)	22.2 3.6 ± 10.3 (1-50)	10.5 4.3 ± 4.3 (1-13)	62.6 5.5 ± 5.8 (1-32)	28.9 24.8 ± 20.4 (2-62)
Enteric Parasite *Bunodera luciopercae*	cladoceran/ amphipod ingestion	intestine	0	0	6.06 8.5 ± 12.2 (1-33)	0	0	0

Crepidostomum cooperi	benthic insect larva ingestion	intestine	36.5 53.6 ± 121.5 (1-578)	8.4 35.4 ± 48.8 (1-212)	0	2.1 2 ± 1.4 (1-3)	0	0
Centrovarium lobotes	fish ingestion	intestine	9.57 ± 4.7 (2-15)	9.8 5.9 ± 4.3 (1-14)	0	0	0	0
Cyathocephalus truncatus	amphipod ingestion	intestine	0	0	0	1.05 2 (2)	0	7.8 1 (1)
Bothriocephalus cuspidatus	copepod ingestion	intestine	19.0 11.9 ± 16.9 (1-58)	11.7 20.6 ± 23.4 (1-85)	7.07 79.7 ± 80.0 (1-221)	1.05 1 (1)	0	0
Proteocephalus pearsei	copepod ingestion	intestine	8.0 18.9 ± 45.3 (1-200)	23.5 25.5 ± 27.5 (1-121)	14.1 45.2 ± 65.2 (1-189)	4.2 2 ± 1.41 (1-4)	2.8 1 (1)	5.2 1.5 ± 0.70 (1-2)
Camallanus oxycephalus	copepod ingestion	intestine	0	0	0	3.1 1.3 ± 0.57 (1-2)	1.8 2 (2)	0
Dichelyne cotylophora	fish ingestion	intestine	0	0	0	0	1.8 1.5 ± 0.70 (1-2)	0
Spinitectus gracilis	insect larvae ingestion	Intestine	25.3 5.1 ± 6.5 (1-23)	27.4 3.7 ± 2.8 (1-13)	7.07 1.4 ± 0.7 (1-3)	0	0	5.2 1 (1)
Echinorhynchus salmonis	amphipod ingestion	Intestine	0	0	0	0	3.7 1.7 ± 0.9 (1-3)	81.5 8.7 ± 15.6 (1-64)
Neoechinorhynchus sp.	amphipod ingestion	intestine	0	0	0	0	0	2.6 1 (1)
Pomphorhynchus bulbocolli	amphipod ingestion	intestine	3.1 1.5 ± 0.7 (1-2)	3.9 1.5 ± 0.5 (1-2)	0	0	0	0

Table 5. Similarity among parasite component communities of yellow perch collected from localities in Manitoba and Wisconsin. Values in parentheses are the number of species observed in each component community, values above the diagonal are the number of species shared between samples, values below the diagonal are Renkonen's percent similarity calculated using the software SIMILAR written by Krebs (1989).

Sample (# species)	Dauphin 1992 (18)	Dauphin 1993 (18)	Beaufort Lake (16)	Lake Winnebago (14)	Green Bay (10)	Lake Michigan (10)
Dauphin 1992 (18)	N/A	18	12	9	5	7
Dauphin 1993 (18)	0.88	N/A	12	9	5	7
Beaufort Lake (16)	0.33	0.35	N/A	8	6	7
Lake Winnebago (14)	0.31	0.27	0.50	N/A	7	6
Green Bay (10)	0.22	0.29	0.09	0.20	N/A	6
Lake Michigan (10)	0.26	0.26	0.09	0.49	0.32	N/A

Table 6. Observed total species richness of parasite assemblages of yellow perch (*Perca flavescens*) from 6 localities. Estimates of total richness were calculated by jackknife procedures as written by Krebs (1987) and bootstrap procedures as written by Pisces Conservation Ltd.

	Dauphin 1992 n = 63	Dauphin 1993 n = 102	Beaufort Lake n = 99	Lake Winnebago n = 95	Green Bay n = 107	Lake Michigan n = 38
observed # species	18	18	16	14	10	10
jackknife	19 ± 0.98	20 ± 1.39	17 ± 0.99	18 ± 2.79	11 ± 0.99	11 ± 0.97
bootstrap	19.9	20.2	16.8	16.0	11.9	10.8

Table 7. Infection statistics for parasite infections of yellow perch collected from 6 different localities

All Parasites	Dauphin Lk.1992 (n = 63)	Dauphin Lk. 1993 (n = 102)	Beaufort Lk. (n = 99)	Lk. Winnebago (n = 95)	Green Bay (n = 107)	Lk. Michigan (n = 38)
All parasites						
# infected hosts	61	98	94	61	102	38
(prevalence %)	(96.8)	(96)	(94.9)	(64.2)	(95.3)	(100)
Total # species	18	18	15	14	10	10
Mean species	5.0 ± 2.4	3.5 ± 2.1	2.1 ± 1.4	1.3 ± 0.7	2.4 ± 1.1	3.4 ± 1.2
richness (range)	(1 - 13)	(1 - 13)	(1 - 7)	(1 - 4)	(1 - 6)	(1 - 6)
Mean intensity	58.7 ± 121.4	37.6 ± 50.2	27.6 ± 66.5	5.0 ± 5.77	10.3 ± 8.1	42.2 ± 44.5
(range)	(1 - 827)	(1 - 300)	(1 - 442)	(1 -29)	(1 -52)	(2 - 238)
Mean abundance	56.8 ± 119.9	35.4 ± 49.5	26.2 ± 65.1	3.2 ± 5.2	9.8 ± 8.2	42.2 ± 44.5
Enteric species						
# infected hosts	46	55	22	10	10	32
(prevalence %)	(73)	(53.9)	(22.2)	(10.5)	(9.3)	(84.2)
Total # species	6	6	4	5	4	5
Proportional abundance	0.64	0.50	0.52	0.06	0.02	0.17
Mean species	2.1 ± 1.2	1.6 ± 1.0	1.5 ± 0.9	1.1± 0.3	1.1 ± 0.3	1.2 ± 0.6
richness (range)	(1 - 6)	(1 - 5)	(1 - 4)	(1- 2)	(1 - 2)	(1 - 4)
Mean intensity	51.0 ±126.2	30.3 + 48.1	56.9 ± 114	1.9 ± 1.1	1.8 ± 0.7	8.7 ± 11.7
(range)	(1 - 783)	(1 - 267)	(1 - 412)	(1 - 4)	(1 - 3)	(1 - 64)
Mean abundance	38.5 ± 111.5	16.3 ± 38.3	12.5 ± 57.3	0.2 ± 0.6	0.1 ± 0.5	7.3 ± 11.2

Allogenic species						
# infected hosts	61 (96.8)	50	83	44	11	30
(prevalence %)		(49)	(83.8)	(46.3)	(10.2)	(78.9)
Total # species	4	4	5	3	2	2
Proportional abundance	0.07	0.07	0.41	0.69	0.04	0.52
Mean species	1.5 ± 0.6	1.2 ± 0.4	1.1 ± 0.3	1.2 ± 0.4	1	1 ± 0.2
richness (range)	(1 – 4)	(1 - 3)	(1 - 2)	(1 – 2)	1	(1 - 2)
Mean intensity	6.4 ± 4.6	4.8 ± 4.9	12.9 ± 14.3	4.8 ± 5.9	3.1 ± 2.8	27.7 ± 35.8
(range)	(1 - 23)	(1 - 26)	(1-72)	(1 - 28)	(1 - 9)	(1 -174)
Mean abundance	6.2 ± 4.6	2.3 ± 4.1	10.8 ± 14	2.2 ± 4.7	0.3 ± 1.3	21.8 ± 33.7
Ectoparasites						
# infected hosts	46	51	34	3	89	32
(prevalence %)	(73)	(50)	(34.3)	(3.1)	(83.1)	(84.2)
Total # species	5	5	4	2	2	2
Proportional abundance	0.11	0.12	0.04	0.04	0.48	0.14
Mean species	1.7 ± 0.8	1.5 ± 0.8	1.1 ± 0.3	11	1.6 ± 0.4	1.2 ± 0.6
richness (range)	(1 - 4)	(1 - 5)	(1 - 2)		(1 - 2)	(1 - 4)
Mean intensity	7.3 ± 7.7	9.2 ± 8.7	4.2 ± 5.4	4.3 ± 3.2	6.1 ± 4.5	8.7 ± 11.7
(range)	(1 - 39)	(1 - 43)	(1 - 30)	(2 - 8)	(1 -21)	(1 - 64)
Mean abundance	5.3 ± 7.3	4.6 ± 7.7	1.4 ± 3.7	0.1 ± 0.8	5.1 ± 4.7	7.3 ± 11.2

Table 8. Comparisons of host size and age of yellow perch from 6 samples*. Fish of indeterminate age were omitted from the analyses. Values indicated are mean $\pm$ standard deviation followed by range in brackets.

	Dauphin Lake 1992 (n = 57)	Dauphin Lake 1993 (n = 101)	Beaufort Lake (n = 88)	Lake Winnebago (n = 95)	Green Bay (n = 97)	Lake Michigan (n = 35)
Length (mm)	129 $\pm$ 64.7 (51 - 301)	193 $\pm$ 28 (51 - 313)	169 $\pm$ 26.5 (130 - 225)	198 $\pm$ 39.5 (108 - 298)	146 $\pm$ 29.7 (99 - 248)	200 $\pm$ 12.6 (175 - 243)
Weight (gm)	55 $\pm$ 82.5 (2 - 351)	98 $\pm$ 45.7 (26 - 349)	64 $\pm$ 25.7 (30 - 137)	153 $\pm$ 89.9 (25 - 382)	52 $\pm$ 35.3 (13 - 200)	108 $\pm$ 24.8 (76 - 189)
Age	1.5 $\pm$ 1.6 (0 - 8)	2.9 $\pm$ 1.1 (1 - 8)	3.1 $\pm$ 1.2 (1 - 7)	2.3 $\pm$ 1.1 (1 - 6)	1.9 $\pm$ 1.1 (1 - 5)	5 $\pm$ 1.3 (3 - 8)

* Date of capture can affect the estimate of size at age. Fish of the same year class captured in May will not have started that years growth while those captured in August will have almost completed that years growth, yet both will be given the same age class designation.

Table 9. Results from multiple regression of fish length, age and sex of the variable fish length on richness and intensity for all parasite species, enteric species only, allogenic species only, and ectoparasites only, respectively. Significance indicated only when $p \leq 0.05$. NS denotes no significant correlation. r^2 denotes the adjusted r^2 for all independent variables, b denotes the standardized coefficient for length, and p denotes the significance with degrees of freedom noted in subscript.

	Dauphin Lake 1992 n = 63	Dauphin Lake 1993 n = 102	Beaufort Lake n = 99	Lake Winnebago n = 95	Green Bay n = 107	Lake Michigan n = 38
Total species richness	$r^2 = 0.33$ $\beta = 0.88$ $p_{1,59} = 0.01$	$r^2 = 0.08$ $\beta = 0.22$ $p_{1,98} = 0.02$	$r^2 = 0.19$ $\beta = 0.69$ $p_{1,95} = 0.0001$	NS	NS	$r^2 = 0.11$ $\beta = 0.39$ $p_{1,34} = 0.03$
Total species intensity	$r^2 = 0.51$ $\beta = 0.74$ $p_{1,59} = 0.02$	NS	$r^2 = 0.05$ $\beta = 0.43$ $p_{1,95} = 0.008$	NS	$r^2 = 0.12$ $\beta = 0.24$ $p_{1,103} = 0.02$	NS
Enteric species richness	NS	NS	$r^2 = 0.09$ $\beta = 0.45$ $p_{1,95} = 0.004$	NS	NS	NS

Enteric species intensity	NS	NS	NS	NS	NS	NS
Allogenic species richness	NS	NS	NS	NS	NS	NS
Allogenic species intensity	NS	$r^2 = 0.15$ $\beta = 0.41$ $p_{1,98} = 0.0001$	$r^2 = 0.15$ $\beta = 0.68$ $p_{1,95} = 0.0001$	NS	NS	NS
Ectoparasite species richness	$r^2 = 0.33$ $\beta = 1.08$ $p_{1,59} = 0.004$	NS	$r^2 = 0.11$ $\beta = 0.46$ $p_{1,95} = 0.003$	NS	NS	NS
Ectoparasite species intensity	$r^2 = 0.31$ $\beta = 1.03$ $p_{1,59} = 0.01$	NS	NS	NS	NS	NS

Table 10. Results from multiple regression of fish length, age and sex of the variable fish age on richness and intensity for all parasite species, enteric species only, allogenic species only, and ectoparasites only, respectively. Significance indicated only when $p \leq 0.05$. NS denotes no significant correlation. r^2 denotes the adjusted r^2 for all independent variables, β denotes the standardized coefficient for length, and p denotes the significance with degrees of freedom noted in subscript.

	Dauphin Lake 1992 n = 57	Dauphin Lake 1993 n = 101	Beaufort Lake n = 88	Lake Winnebago n = 95	Green Bay n = 97	Lake Michigan n = 35
Total species richness	NS	NS	$r^2 = 0.19$ $\beta = -0.35$ $p_{1, 84} = 0.01$	NS	NS	$r^2 = 0.11$ $\beta = -0.55$ $p_{1, 31} = 0.01$
Total species intensity	NS	$r^2 = 0.15$ $\beta = 0.33$ $p_{1, 97} = 0.001$	NS	NS	NS	$r^2 = 0.15$ $\beta = -0.63$ $p_{1, 31} = 0.004$
Enteric species richness	NS	NS	NS	NS	NS	NS

Enteric species intensity	NS	NS	NS	NS	NS	NS
Allogenic species richness	NS	NS	$r^2 = 0.15$ $\beta = -0.50$ $p_{1, 84} = 0.001$	NS	NS	NS
Allogenic species intensity	NS	NS	NS	NS	NS	NS
Ectoparasite species richness	$r^2 = 0.33$ $\beta = -0.81$ $p_{1, 53} = 0.02$	NS	NS	NS	NS	NS
Ectoparasite species intensity	$r^2 = 0.26$ $\beta = -0.77$ $p_{1, 53} = 0.04$	$r^2 = 0.07$ $\beta = 0.27$ $p_{1, 97} = 0.01$	NS	NS	NS	NS

Table 11. Results from multiple regression of fish length, age and sex of the variable fish sex on richness and intensity for all parasite species, enteric species only, allogenic species only, and ectoparasites only, respectively. Significance indicated only when $p \leq 0.05$. NS denotes no significant correlation. r^2 denotes the adjusted r^2 for all independent variables, β denotes the standardized coefficient for length, and p denotes the significance with degrees of freedom noted in subscript.

	Dauphin Lake 1992 n = 57	Dauphin Lake 1993 n = 101	Beaufort Lake n = 88	Lake Winnebago n = 95	Green Bay n = 97	Lake Michigan n = 35
Total species richness	$r^2 = 0.33$ $\beta = 0.44$ $p_{1,53} = 0.002$	NS	NS	NS	NS	NS
Total species intensity	$r^2 = 0.51$ $\beta = 0.30$ $p_{1,53} = 0.01$	NS	NS	NS	NS	NS

Enteric species richness	NS	NS	NS	NS	NS	NS
Enteric species intensity	NS	NS	NS	NS	NS	NS
Allogenic species richness	NS	NS	NS	NS	NS	NS
Allogenic species intensity	$r^2 = 0.20$ $\beta = -0.33$ $p_{1, 53} = 0.02$	NS	NS	NS	NS	NS
Ectoparasite species richness	$r^2 = 0.33$ $\beta = 0.59$ $p_{1, 53} = 0.001$	NS	$r_S = 0.20$ $z = 2.02$ $p = 0.04$	NS	NS	NS
Ectoparasite species intensity	$r^2 = 0.26$ $\beta = 0.52$ $p_{1, 53} = 0.001$	NS	NS	NS	NS	NS

Table 12. Chi-square comparison of observed frequency distributions to expected distributions for 6 species of enteric parasites in 63 *Perca flavescens* collected in 1992 from Dauphin Lake, Manitoba.

Parasite community*	Observed (number of perch)	Expected (number of perch)	X^2
Empty	17	9.19	6.64
1	1	0.97	0.0009
2	3	6.89	2.19
3	0	3.13	3.13
4	7	7.35	0.02
5	6	3.67	1.48
6	1	0.46	0.63
any 2 spp.	14	20.61	2.12
any 3 spp.	8	8.81	0.07
> 3 spp.	6	1.93	8.58
			$X^2_{tot.} = 24.8$
			$X^2_{crit.} = 16.9$
			$p = 0.003$

*1, *Centrovarium lobates*; 2, *Crepidostomum cooperi*; 3, *Bothriocephalus cuspidatus*; 4, *Proteocephalus pearsei*; 5, *Spinitectus gracilis*; 6, *Pomphorhynchus bulbocolli.*

Table 13. Chi-square comparison of observed frequency distributions to expected distributions for 6 species of enteric parasites in 102 *Perca flavescens* collected in 1993 from Dauphin Lake, Manitoba.

Parasite community*	Observed (number of perch)	Expected (number of perch)	X^2
Empty	47	37.23	2.56
1	1	4.04	2.29
2	10	12.08	0.36
3	1	3.17	1.48
4	10	9.07	0.09
5	10	12.74	0.59
6	0	1.12	0.99
any 2 spp.	16	18.33	0.29
any 3 spp.	2	3.81	0.86
> 3 spp.	5	0.41	51.19
			$X^2_{tot.} = 60.8$
			$X^2_{crit.} = 16.9$
			$p = 0.0001$

*1, *Centrovarium lobates*; 2, *Crepidostomum cooperi*; 3, *Bothriocephalus cuspidatus*; 4, *Proteocephalus pearsei*; 5, *Spinitectus gracilis*; 6, *Pomphorhynchus bulbocolli*.

Table 14. Chi-square comparison of observed frequency distributions to expected distributions for 4 species of enteric parasites in 99 *Perca flavescens* collected in 1992 from Beaufort Lake, Manitoba.

Parasite community*	Observed (number of perch)	Expected (number of perch)	X^2
Empty	77	68.96	0.93
1	2	4.45	1.35
2	0	5.25	5.25
3	9	11.36	0.49
4	4	5.25	0.29
any 2 spp.	3	3.53	0.08
> 2 spp.	4	0.21	68.40
			$X^2_{tot.} = 76.79$
			$X^2_{crit.} = 12.59$
			$p = 0.0001$

*1, *Bunodera luciopercae*; 2, *Bothriocephalus cuspidatus*; 3, *Proteocephalus pearsei*; 4, *Spinitectus gracilis*.

Table 15. Chi-square comparison of observed frequency distributions to expected distributions for 5 species of enteric parasites infecting *Perca flavescens* collected 1992 from Lake Winnebago, Wisconsin. Ninety-five fish were examined, 10 were infected.

Parasite community*	Observed (number of perch)	Expected (number of perch)	X^2
Empty	85	84.6	0.002
1	2	1.74	0.04
2	0	0.9	0.9
3	4	3.71	0.02
4	3	2.71	0.03
5	0	0.9	0.9
> 1 spp.	1	0.46	0.64
			$X^2_{tot.} = 2.53$
			$X^2_{crit.} = 12.59$
			$p = 0.864$

*1, *Crepidostomum cooperi*; 2, *Bothriocephalus cuspidatus*; 3, *Proteocephalus pearsei*; 4, *Camallanus lacustris*; 5, *Cyathocephalus truncatus*.

Table 16. Chi-square comparison of observed frequency distributions to expected distributions for 6 species of enteric parasites in *Perca flavescens* collected in 1992 from Green Bay, Wisconsin. One hundred seven fish were examined, 10 were infected.

Parasite community*	Observed (number of perch)	Expected (number of perch)	X^2
Empty	97	96.47	0.003
1	2	2.78	0.22
2	1	.88	0.02
3	3	3.71	0.13
4	3	2.78	0.02
> 1 spp.	1	.38	1.01
			$X^2_{tot.} = 1.40$
			$X^2_{crit.} = 11.07$
			$p = 0.9272$

*1, *Proteocephalus pearsei*; 2, *Camallanus lacustris*; 3, *Echinorhynchus salmonis*; 4, *Dichelyne cotylophora*

Table 17. Chi-square comparison of observed frequency distributions to expected distributions for 5 species of enteric parasites in 38 *Perca flavescens* collected in 1992 from Lake Michigan, Wisconsin

Parasite community*	Observed (number of perch)	Expected (number of perch)	X^2
Empty	6	5.67	0.02
1	0	0.31	0.31
2	1	0.48	0.56
3	0	0.31	0.31
4	0	0.15	0.15
5	26	24.99	0.04
any 2 spp.	4	5.62	0.47
> 3 spp.	1	0.46	0.63
			$X^2_{tot.} = 2.49$
			$X^2_{crit.} = 14.06$
			$p = 0.9274$

*1, *Proteocephalus pearsei*; 2, *Cyathocephalus truncatus*; 3, *Spinitectus gracilis*; 4, *Neoechinorhynchus* sp. 5, *Echinorhynchus salmonis*.

Table 18. Comparison of nestedness between observed matrices of parasite species presence-absence and the distribution of 500 randomly generated matrices based on the same proportion of parasite species presence in each sample. Fill refers to the proportion of the overall matrix with parasite species present. T is a value representing the degree of nestedness where 0 represents complete nestedness and 100 represents complete disorder. Significance determined by z-score.

	Dauphin Lake 1992	Dauphin Lake 1993	Beaufort Lake	Lake Winnebago	Green Bay	Lake Michigan
Observed fill	26.3%	18.5%	13.4%	9.9%	23.6%	34.4%
Observed T	22.35	16.96	6.6	7.91	7.99	14.11
Simulated T*	60.9 ± 3.84	51.1 ± 3.23	37.2 ± 3.32	23.7 ± 3.48	51.8 ± 4.29	54.8 ± 5.81
Significance	0.0001	0.0001	0.0001	0.0001	0.001	0.0001

Mean value ± S.D. based on 500 randomly generated matrices having the same proportion of fill as the observed matrix.

Table 19. Stomach contents of perch collected from each of 5 lakes. Numbers indicate the number of fish with each food category. Values can exceed 100%.

Stomach contents	Dauphin Lake 1992 n = 63	Dauphin Lake 1993 n = 102	Beaufort Lake n = 99	Lake Winnebago n = 95	Green Bay n = 107	Lake Michigan n = 38
Empty	20 (32%)	27 (26%)	23 (23%)	29 (30%)	15 (14%)	29 (76%)
Pelagic						
Fish	24 (38%)	54 (53%)	38 (38%)	0	1 (1%)	7 (18%)
Cladocera	19 (30%)	25 (24%)	0	35 (37%)	0	0
Coleoptera	0	1 (1%)	5 (5%)	0	2 (2%)	0
Benthic						
Amphipoda	2 (3%)	2 (2%)	25 (25%)	0	0	0
Trichoptera larvae	0	0	8 (8%)	0	0	0
Chironomid larvae	0	0	6 (6%)	14 (15%)	64 (60%)	0

Hymenoptera	0	1 (1%)	0	0	0	0
Odonata larvae	0	0	6 (6%)	0	0	0
Ephemeroptera larvae	0	0	4 (4%)	0	0	0
Unidentified insect larvae	9 (14%)	28 (27%)	8 (8%)	7 (7%)	20 (19%)	2 (5%)
Clam	0	0	0	3 (3%)	0	0
Leech	0	0	1 (1%)	0	0	0
Fish eggs	0	0	5	0	1 (1%)	0
Seeds	0	0	0	21 (22%)	0	0
Total types	4	6	10	5	5	2

CHAPTER 3

The core-satellite hypothesis: a test using yellow perch parasite communities

ABSTRACT: The core-satellite species hypothesis (Hanski, 1982a) predicts bimodality in the frequency distribution of species, a positive correlation between distribution and abundance, and switching of species between the core and satellite modes. This concept has been widely adopted by parasitologists but has never explicitly been tested using parasite data. The validity of this hypothesis is tested using parasite communities of yellow perch. Analysis at the continental scale of 37 parasite communities does not reveal a core-satellite dichotomy. There is a positive correlation between distribution and abundance. Analysis of each local community, defined here as the individual lake from which the fish were sampled, revealed 8 of 37 local communities with evidence of bimodal pattern of species distribution. If present, core species were dominated by non-host-specific parasite species. Taxonomic differences among the core taxa provide evidence of core-satellite switching among sites. Only 4 local communities had a positive correlation between distribution and abundance. While parasites meet the assumptions of the model and therefore provide a valid test of this hypothesis, the core-satellite hypothesis is not supported by yellow perch parasite communities at a continental scale and infrequently at the local scale.

INTRODUCTION

The core-satellite hypothesis (Hanski, 1982a) predicts a bimodal frequency distribution of species abundances for many communities of ecologically similar organisms and is derived from a dynamic model based on stochastic rates of local immigration and extinction. This model is based on the positive correlation between species abundance and distribution. Specifically, species that occur at many sites tend also to be abundant within sites, whereas species that occur at few sites tend to be rare within sites. Predictions of this model include a bimodal pattern of species distribution. One mode has species with low local abundances, which occur, at few locations. These are designated satellite species. The second mode is smaller and is comprised of species that are locally abundant and occur at almost all of the locations. Species in this mode are called core species. The core-satellite hypothesis also predicts there will be switching between core and satellite species over time, as well as a positive correlation between distribution and abundance. A similar model, also based on stochastic immigration and extinction rates, was provided by Levins (1969). This model predicts a unimodal distribution of species occurrence and does not

predict a positive correlation between distribution and abundance (Levins, 1969).

Tests of the core-satellite hypothesis have produced conflicting results. Studies supporting the hypothesis are from mangrove insects, anthropochorous plants, and rain forest insects (Hanski, 1982a), bumblebees (Hanski, 1982b), tall grass prairie plants (Gotelli and Simberloff, 1987) and grassland vegetation (Collins and Glen, 1990; 1991). By contrast, Gaston and Lawton (1989) could not support the core-satellite hypothesis for communities of phytophagous insects and questioned the validity of previous studies. Brown (1984, 1995) argued that observed correlations between distribution and abundance and bimodal patterns of species distribution result from niche-based requirements and not from metapopulation dynamics. Species with broad-based niches would be widespread and occur at most sites. Specialized species with narrow niches would occur at a more restricted set of sites.

The core-satellite hypothesis was introduced into the parasitological literature by Bush and Holmes (1986a) and Holmes and Price (1986). Core species were considered to be those parasites that occur frequently and have high abundance (Holmes and Price, 1986). Satellite species occur infrequently among hosts and are not numerous within them. The core-

satellite hypothesis is widely applied as a concept to describe parasite community structure (Table 20). The only parasite studies in which the presence of a bimodal distribution and correlation between distribution and abundance were tested are those of Bush and Holmes (1986a) and Stock and Holmes (1987). However, core species were designated based solely on prevalence greater than 70%, irrespective of the presence or absence of bimodal distributions. Other studies in which this concept has been applied have been inconsistent in the use of frequency of occurrence. For example, species have been designated as core based on prevalence ranging from 30% (Roca and Hornero, 1992), 40 and 50% (Goldberg et al., 1995), 60% (Cislo and Caira, 1993), 70% (Stock and Holmes, 1987) and 80% (Aho et al., 1991). The core mode also has been identified based on fecundity and transmission parameters (Dobson and Pacala, 1992), scatterplots of intensity vs. prevalence (Bursey and Goldberg, 1994; Goldberg et al., 1995), and host specificity and wide distribution (Coyner et al., 1996). Clearly, parasitologists find the concept to have utility, but such inconsistencies in definition and application make it difficult to assign biological relevance to the application and interpretation of this model.

Designating a parasite species as core is often based on host specificity (e.g. Coyner et al., 1996). If a parasite is host-specific the

definition of the core is modified to include that species (e.g. Bush and Holmes, 1986a). Parasite species that are not host-specific are then considered to be satellite species. Switching between core and satellite modes as predicted by this model would therefore require a change in host specificity. Furthermore, this imposes the assumption that host specificity is required for predictability since those species in the core mode are present with sufficient frequency to be considered predictable.

Yellow perch are recorded as host to a large list of parasites (Hoffman, 1967; Margolis and Arthur, 1979; McDonald and Margolis, 1995) potentially allowing for speciose communities to exist. There are predictable suites of parasites at the continental and local scales (Chapters 1 and 2). Transmission through feeding habits on a rich invertebrate fauna capable of transmitting parasites might be responsible for this predictability. The core-satellite hypothesis is an alternate explanation for this predictability that is based on stochastic rates of immigration and extinction.

METHODS AND MATERIALS

Original data came from parasite surveys of yellow perch from Dauphin Lake and Beaufort Lake in Manitoba, and Lake Winnebago, Green Bay and Lake Michigan in Wisconsin. The criteria for including a data set from the literature were a minimum of 10 hosts had to have been examined for parasites from a single designated location. This is considered to be a local sample and represents the parasites present in a discrete population of perch. In addition, the actual number of hosts infected with each parasite had to be reported. Prevalence (Margolis et al., 1982) was calculated for analysis of local samples.

For each sample, a frequency distribution of parasite species presence was calculated based on parasite prevalence. Continental analysis was performed by pooling the local samples. Region is defined as the geographic range of yellow perch. The presence of the parasite in a sample was sufficient for its inclusion in the continental analysis, regardless of its prevalence within a sample. This permitted the inclusion of additional data sets for which the local prevalence was not recorded.

All studies included an examination for enteric parasites, but not all studies included in this analysis reported ectoparasites such as monogeneans or copepods, or larval stages encysted in viscera, eyes, or musculature.

Consequently, the prevalence of non-enteric parasites was calculated as a proportion of all studies in which examination for these types of parasites were undertaken.

The correlation between prevalence and intensity was calculated (Abacus Concepts, 1992) to determine if the assumption of a positive correlation between distribution and abundance was met. Only those studies for which these data were available were included in this analysis at the level of the local community. All studies were included at the continental level and the correlation was between the number of samples in which the parasite species occurred and the number of infected fish within each sample.

The terms specialist and generalist have frequently been used to contrast host-specific and non host-specific parasites (see Table 1). Although different parasites may have specialized attributes that are unrelated to host specificity, in order to maintain consistency with these previous studies, a specialist parasite is defined here as one that infects just a single host species (i.e. host-specific). Implicit in this definition is the ability to reproduce. Being a specialist does not preclude rare, accidental, infections in an anomalous host. For example, Poole (1985) reported the presence of a single *Lissorchis kritskyi* Barnhart and Powell, 1979 in one yellow perch, but this parasite is a specialist of catastomids; the report was an accidental infection

of an atypical host. Such a parasite is considered here to be an accidental infection. Parasites in this category generally have been reported from a single fish, or from several fish at low levels of infection from a single locality by a single author(s). A generalist parasite is one that is not host-specific but occurs frequently in many species. The taxonomy of the original authors is accepted with corrections for published synonymies.

RESULTS

Results of the continental analysis for the frequency distribution of 78 parasite species among 3100 fish from 37 localities are shown in Figure 4. Clearly at this spatial scale there is no evidence for a bimodal distribution of species abundances. The majority of species occur in fewer than 10% of the samples. There were no species occurring in 90% or more of the samples and very few occurred in 70-90% of samples. This distribution most closely resembles a log-series distribution and is consistent with the unimodal distribution predicted by Levins (1969). There is a positive correlation between distribution and abundance (Table 21). This correlation is not predicted by Levins (1969) but is consistent with the prediction made by Hanski (1982a).

Frequency distributions for each local sample were plotted (Figure 5). Eight of the samples did have bimodal distributions while the remainder had a variety of forms. The White Sand Lake sample (Bangham, 1944) provides the best approximation of the bimodal distribution predicted by Hanski (1982a). Appropriate data were not available to analyze for a correlation between distribution and abundance from the majority of samples. Of 11 samples for which suitable data are available, there is a significant positive correlation between distribution and abundance in only four (Table 21).

DISCUSSION

There is taxonomic predictability in the parasite communities of yellow perch in North America at different spatial scales (Chapters 2 and 3). Transmission dynamics based on feeding habits are the basis for much of this structure. The core-satellite hypothesis (Hanski, 1982a) also predicts taxonomic predictability based on a bimodal distribution of species abundance for communities of ecologically similar organisms. Species in the core are those that are predictably present among communities. The model is based on stochastic rates of immigration and extinction. My interpretation of Hanski (1982a) is that transmission can be substituted for immigration and the presence of a predictable core in the parasite communities of yellow perch may result from stochastic rates of transmission. Furthermore, it provides an evaluation of the importance of host specificity (= specialist vs. generalist) as used by previous authors.

The parasite communities of yellow perch are characterized by non-host-specific parasites, thereby minimizing the influence of the host-specific parasites. This analysis represents the first time parasites have been used to test this hypothesis. At the continental scale there was a strong correlation between distribution and abundance. Parasites that are widely distributed infect more individual hosts but at the continental scale there is

no evidence for a bimodal distribution of species; there are no core species of parasites of yellow perch over the range sampled. These results are compared with those from Chapter 1, where predictability was demonstrated in the parasite communities of both *Perca flavescens* and *Perca fluviatilis* (Carney and Dick, 1999). Three species (*Urocleidus adspectus*, *Proteocephalus pearsei*, and *Diplostomum* sp.) in the continental analysis occurred at frequencies of 70-90% of the samples. Their frequencies are not high enough to constitute the core mode as defined by Hanski (1982a). This observation supports the point of Bush et al. (1998) that use of the terms core and satellite should be restricted to those studies explicitly testing the hypothesis, or where the species identified meet the criteria outlined by Hanski (1982a). Clearly, the core-satellite hypothesis does not explain the predictable suite of parasites associated with yellow perch at the continental scale (Carney and Dick, 1999).

At the local scale, there is occasional support for the core-satellite hypothesis. The species in the core mode in samples with a bimodal distribution are listed in Table 22. With the exception of *Urocleidus adspectus*, the core species in a local sample are non-host-specific parasites, with four species using piscivorous birds as final hosts. Assuming the required aquatic hosts are present, the presence of bird-transmitted parasites

in a system is primarily a random event dependent on the presence of the bird host (Kennedy and Burrough, 1978). Although parasites belonging to this ecological group generally are predictably present, the specific taxonomic identity of the species differs. Since the core-satellite hypothesis is based on taxonomic predictability, the presence of parasites transmitted to, and dependent on, the presence of the bird host is not relevant to a test of the core-satellite hypothesis using parasites of yellow perch.

The core-satellite hypothesis has been used in studies of parasite communities to determine if parasite communities occur in non-random patterns, i.e., are predictable (core) parasites host-specific? In previous investigations different criteria have been used to identify a core group of parasites, thereby imposing a forced degree of predictability (see Table 20). Furthermore, the criteria designating the core species are often applied to ensure that host-specific parasites will be in the core. This presupposes that host-specific parasites will be in the core, and therefore predictable and that a change in host specificity is required in order to meet the prediction of core-satellite switching.

I found limited support for the predictions of the core-satellite hypothesis. There was no evidence of bimodality of species occurrence at the continental scale but there was a positive correlation between

distribution and abundance. The dynamic model of Levins (1969) did not anticipate this correlation and, as a consequence, the core-satellite model also was not supported. There was no evidence of bimodality in the majority of local samples. There were 8 communities where such a distribution was observed. My data (data collected in North America and reported in this study), where the majority of the core species were not host-specific, support the niche-based predictions of Brown (1984, 1995) where generalist species are those with broad niches and specialist species are those with narrow niches. Species with broad niche requirements would occur in many habitats over a wide spatial range and be common where they occur. By contrast, species with narrow niche requirements would occur in few habitats and these would not be widespread and this would limit their local abundance. In the context of parasites, this is translated as those species capable of infecting many host species and those that are host-specific. Future studies using hosts with a large suite of host-specific parasites would provide a valuable addition to this interpretation of the core-satellite hypothesis as applied to yellow perch. Perhaps, for host-parasite systems, support for the core-satellite hypothesis (Hanski, 1982a) requires host-specific parasites in the communities at whatever scale.

Table 20. Summary of published parasite studies specifically utilizing the core-satellite species hypothesis/concept.

Author	Host type (sample size)	How core was identified	Total number of parasite species	Number of core species	Specialist/ generalist
Bush & Holmes, 1986a	bird (45)	- prevalence bimodality - frequency/abundance correlation	52	8	6 specialist 2 generalist
Bush & Holmes, 1986b	bird (45)	- prevalence bimodality - frequency/abundance correlation	52	8	6 specialist 2 generalist
Forrester et al., 1987	muskrat (114)	- not in local sample - frequency among samples (n = 6)	13	3	3 specialist
Stock & Holmes, 1987	4 bird spp. (96)	- prevalence bimodality - frequency/abundance correlation	34	14	11 specialist 3 generalist
Goater & Bush, 1988	bird (20)	- prevalence - frequency/abundance correlation	9	2	2 specialist
Hinojos & Canaris, 1988	bird (35)	- clustering techniques	19	10	5 generalist (not clear)
Stock & Holmes, 1988	4 bird spp. (96)	- previous study - even in niche space	34	14	not discussed (uneven in niche space)

Kennedy & Bakke, 1989	bird (269)	- frequency distribution of prevalences	33	0	n/a
Aho, 1990	herptiles (n/a)	- prevalence >50%	0-9 amphib. 0-10 reptile 30 total	0-3 amphib. 0-7 reptile 18 total	generalist
Pence, 1990	mammal	- occurrence in all locations	29	2 coyote	generalist
Holmes, 1990	marine fish (88)	- prevalence >60%	27	5 (4-9 in 10 samples)	2 specialist 3 generalist
Aho et al., 1991	bowfin (12)	- prevalence >80%	13	5	3 specialist 2 generalist
Canaris & Munir, 1991	bird (50)	- % total abundance - abundance - prevalence vs intensity	5	none identified	n/a
Kinsella, 1991	3 mice spp. (229)	- high prevalence and high intensity,	19	none identified	n/a
Dobson & Pacala, 1992	lizard (964)	- core: high fecundity, high transmission	9	1? (suggested)	n/a
Roca & Hornero, 1992	lizard	- prevalence >30%			
Balbuena & Rego, 1993	whale (170)	- unimodal distribution of prevalence - no prevalence >60%	8	none identified	n/a
Choudhury & Dick, 1993	fish (223)	- prevalence >70%	19	4	4 specialist
Cislo & Caira, 1993	shark (44)	- prevalence >60%	4	2	not identified

Hartvigsen & Halvorsen, 1993	fish (146)	- regionally widespread locally abundant	9	1	not identified
Secord & Canaris, 1993	bird (48)	- % total abundance - abundance - prevalence vs intensity	9	2	2 generalist
Thoney, 1993	2 fish spp. (297)	- abundance - prevalence >80%	33	3	3 generalist
Bursey & Goldberg, 1994	lizard (549)	- prevalence/intensity scattergram - prevalence >90%	5	1	not addressed
Feydnich & Pence, 1994	bird (205)	- large set with intermediate prevalence	34	none identified	n/a
Goldberg et al., 1995	3 toad spp. (116)	- prevalence/intensity scattergram	5	2	2 generalist
Coyner et al., 1996	2 squirrel ssp. (119)	- host specificity - wide distribution	11	4	not addressed

Table 21. Correlation between distribution and abundance of parasite species in yellow perch analyzed at the continental scale and for local samples from 11 different localities.

	Continental	Home Lk.	Wapun Lk.	Demarch Lk.	Quigley Lk.	Dauphin Lk.
correlation	0.822	0.885	0.760	0.227	0.279	0.279
r^2	0.676	0.783	0.578	0.051	0.078	0.078
p	0.0001	0.0006	0.006	NS	NS	NS

	Beaufort Lk.	Lk. Winnebago	Gr. Bay	Lk. Michigan	Laurel Cr.	Heming Lk.
correlation	-0.006	0.074	0.510	0.496	0.577	
r^2	0.00003	0.006	0.260	0.246	0.333	0.578
p	NS	NS	NS	NS	0.049	0.0002

Table 22. Species in the core mode for 8 local samples with a bimodal distribution of species occurrence. Generalist refers to species which are not host-specific, specialist refers to species which are host-specific. P indicates the presence of the species in the core mode for that local sample.

Parasite species	Type	Carroll Lk	L. John Lk.	Snake Lk.	White Sand Lk.	Pinkeye Lk.	Lk Michigan	Home Lk.	Wapun Lk.
Diplostomum sp.	generalist	P	P		P	P			P
Neascus sp.	generalist	P	P	P	P	P			
Apophallus sp.	generalist						P	P	
Clinostomum sp.	generalist		P						
Proteocephalus pearsei	generalist	P	P	P	P				
Dichelyne cotylophora	generalist	P			P				
Urocleidus adspectus	specialist		P	P			P		
Raphidascaris acus	generalist							P	P

Figure 4. Continental frequency distribution of parasite species of yellow perch from 31 localities.

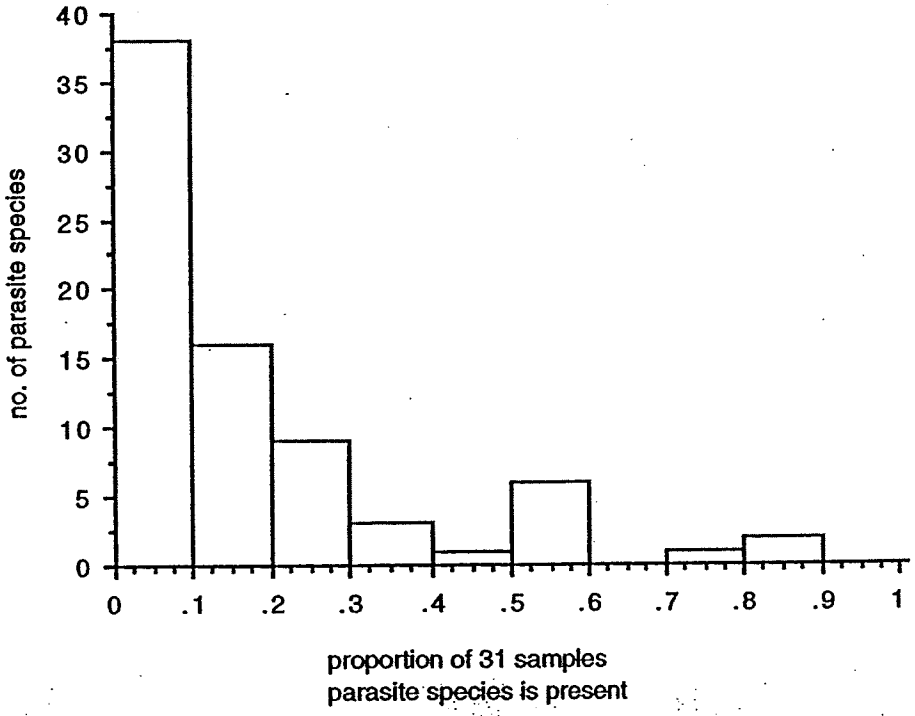
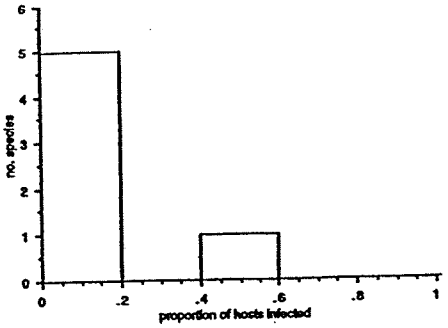
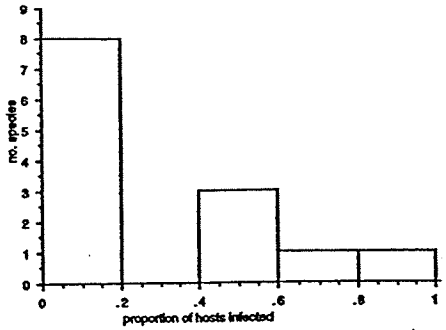

40
35
30
25
20
15
10
5
0
no. of parasite species
0
.1
.2
.3
.4
.5
.6
.7
.8
.9
1
proportion of 31 samples
parasite species is present

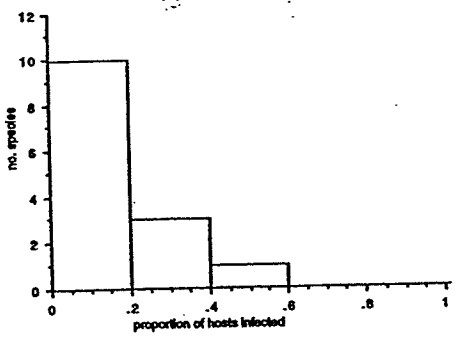
Figure 5. Frequency distribution of parasite species among local yellow perch (*Perca flavescens*) host populations from each of 31 localities. Captions indicate original author and lake or stream identity.



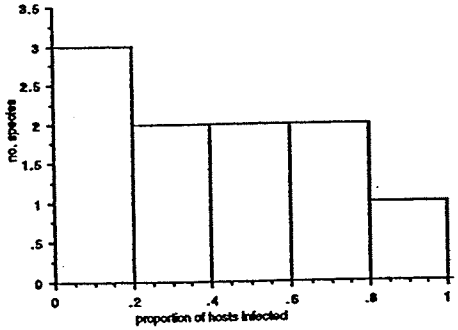
Bangham and Hunter, 1939. East Lake Erie



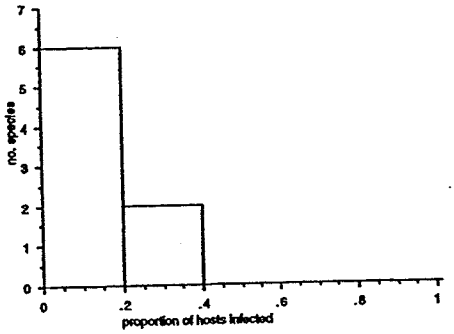
Bangham, 1944. Johnson Lake



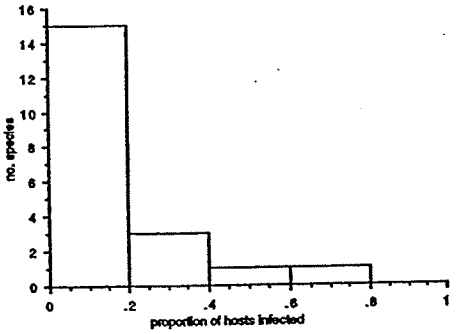
Bangham and Hunter, 1939. Western Lake Erie



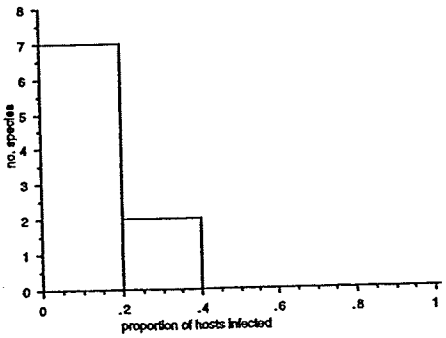
Bangham,1944. Madeline Lake



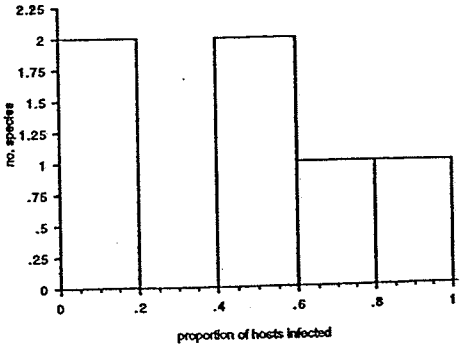
Cannon, 1973. Lake Opeongo



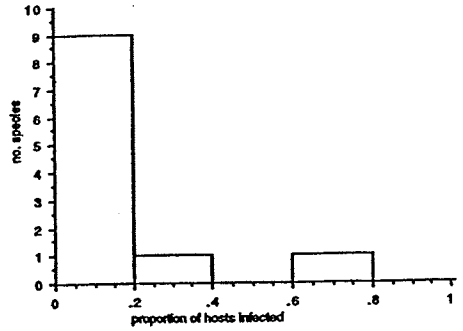
Bangham, 1972. Lake Erie.



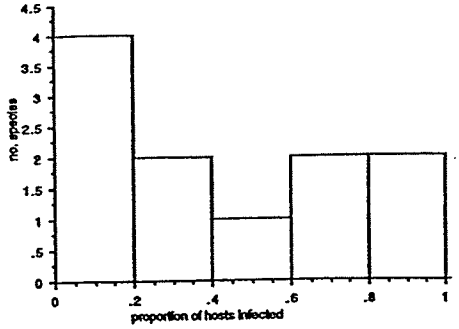
Dechtiar, 1972a. Lake Erie



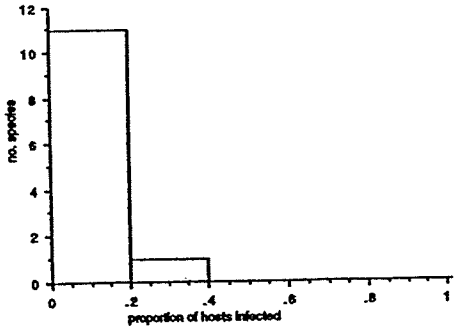
Sutherland and Holloway, Jr., 1979. James R. N. Dakota.



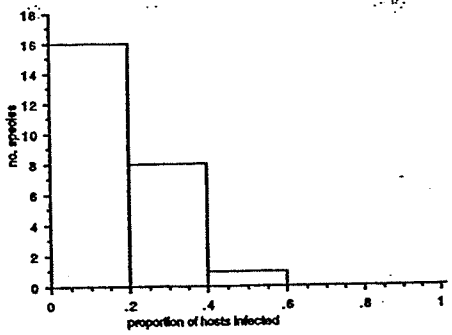
Carney and Dick, 2000. Beaufort Lake



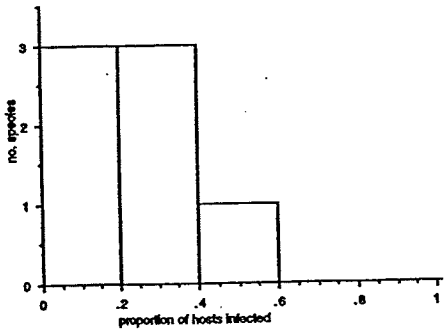
Bangham, 1944. Pinkeye Lake



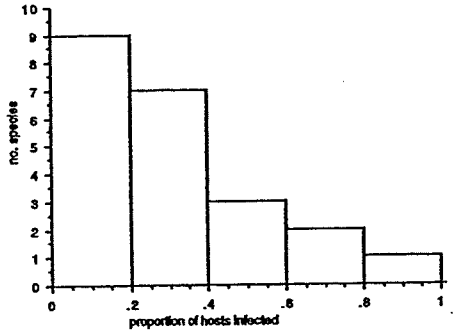
Carney and Dick, 2000. Lake Winnebago



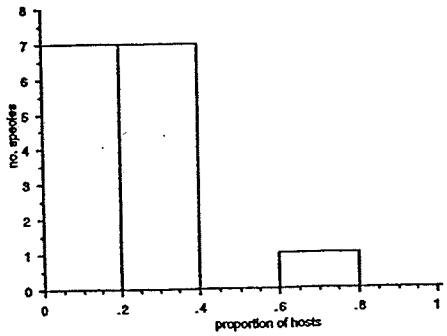
Dechtiar, 1972b. Lake of the Woods



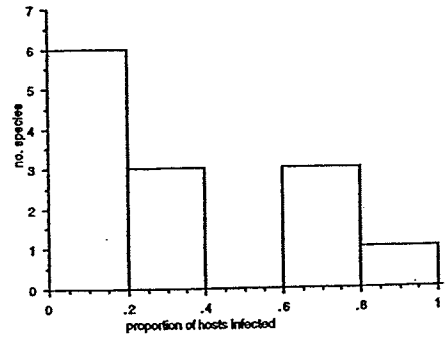
Meyer, 1958. Trumbull Lake Iowa



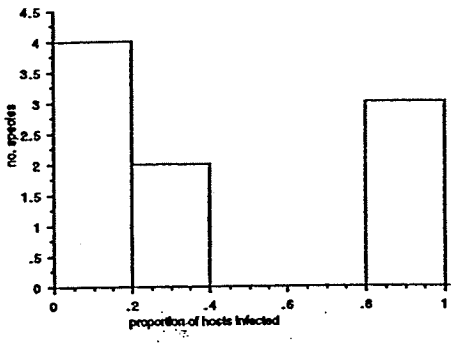
Noble, 1970. Oneida Lake



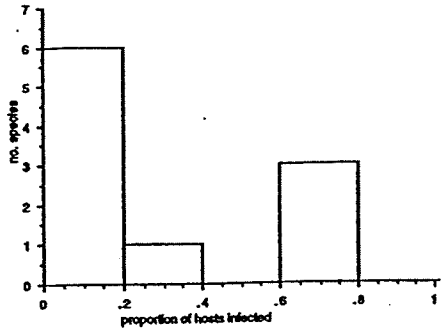
Carney and Dick, 2000. Dauphin Lake



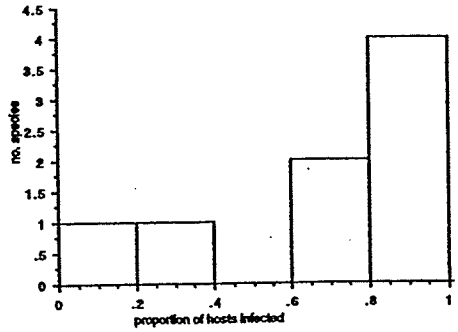
Molnar et al., 1974. Laurel Creek Ontario



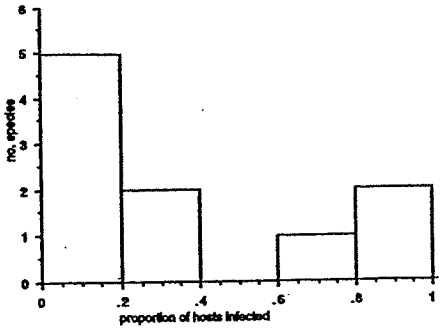
Bangham, 1944. Snake Lake



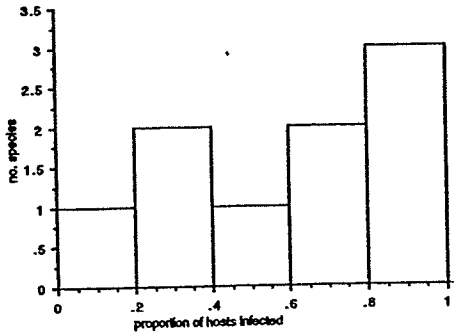
Carney and Dick, 2000. Green Bay



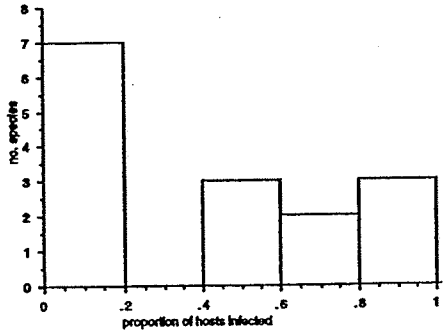
Bangham, 1944. Nabish Lake



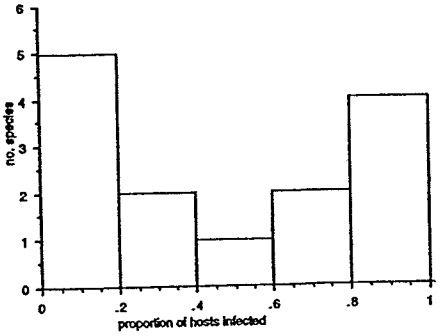
Carney and Dick, 2000. Lake Michigan



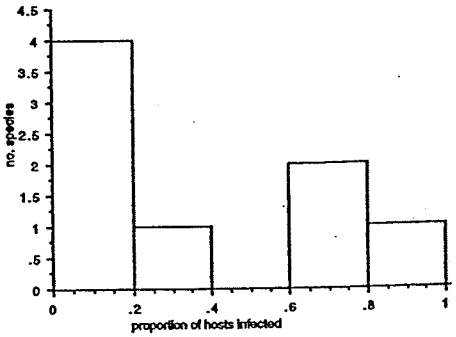
Bangham, 1944. Chetac Lake



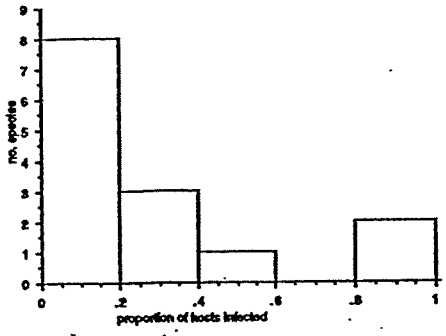
Bangham, 1944. Sweeney Lake



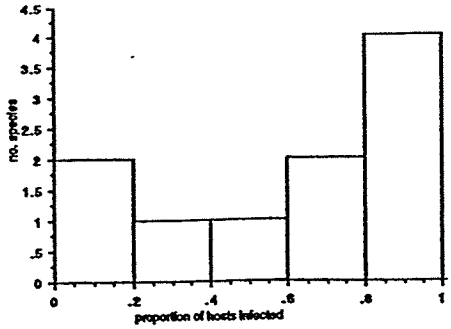
Bangham, 1944. White Sand Lake



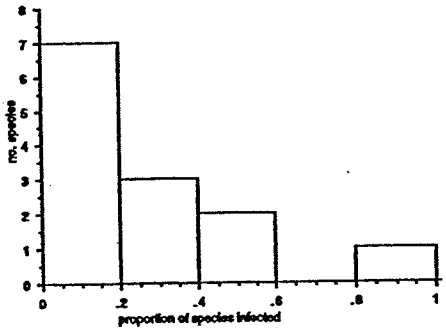
Bangham, 1944. Clear Lake



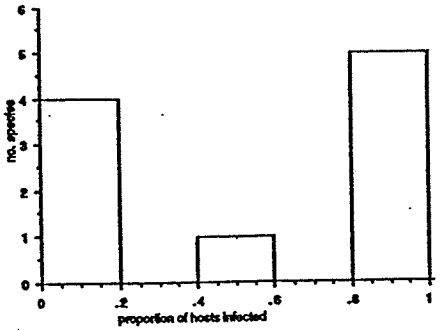
Poole, 1985. Honie Lake



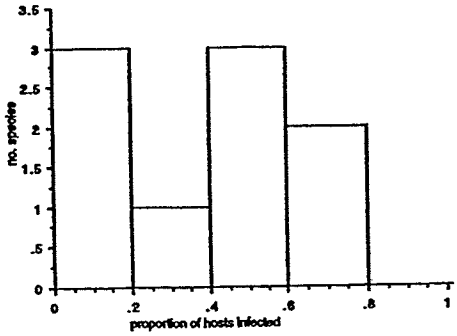
Bangham, 1944. Carroll Lake



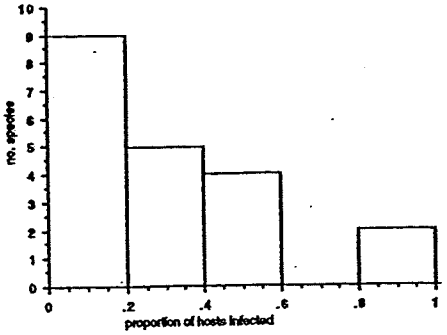
Poole, 1985. Demarch Lake



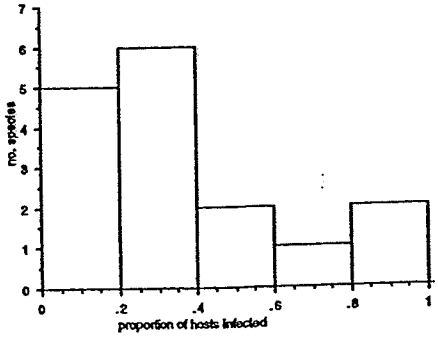
Bangham, 1944. Little John Lake



Poole, 1985. Quigley Lake



Poole, 1985. Heming Lake



Poole, 1985. Wapun Lake

CHAPTER 4

The historical ecology of yellow perch and their parasites

ABSTRACT: The historical ecology of yellow perch and its predicable parasites is examined by incorporating information from host and parasite phylogenetic hypotheses, palaeontology and the fossil record, palaeogeography and plate tectonics and host biology. Although the fossil evidence is limited, there is cumulative information to suggest that the family Percidae is older than generally supposed. The presence of *Perca* in North America is unlikely due to dispersal from Europe or Asia subsequent to speciation. Rather, it reflects a presence that dates at least to the Oligocene, and the present disjunction with Eurasian species is a consequence of vicariance resulting in allopatric speciation. The predictable parasite species in *Perca flavescens* in North America, clearly have an ecological and not a cospeciation origin. Cladistic analysis based on adult morphology of some Nearctic species of the cestode genus *Proteocephalus* from freshwater fishes does not support cospeciation as the origin of the associations between *P. pearsei* and *Perca flavescens* in North America, and *P. luciopercae* and *Perca fluviatilis* in Eurasia. Interpretation of phylogenetic hypotheses that include *Urocleidus adspectus*, *Bunodera luciopercae*, *Crepidostomum cooperi*, and *Dichelyne cotylophora* support the interpretation that the association between these parasite species and yellow perch is a consequence of host-switching and not cospeciation. Host

species from which these parasites were acquired likely share similar ecology, especially shared feeding strategies. This supports non-host specific and non-coevolutionary explanations for the association between yellow perch and its predictable parasites.

INTRODUCTION

Yellow perch (*Perca flavescens*) is found in North America whereas its sister species the perch (*Perca fluviatilis*) is found in Eurasia (Craig, 1987). These two species are very similar in their overall biology, a fact reflected in their patterns of parasitism (Carney and Dick, 1999). In Chapter 1 I demonstrated that there was a suite of parasites, unique to each of the two perch species, that was predictably associated with each host and proposed the basis for this was ecological in nature (Carney and Dick, 1999). However, based on their extant worldwide distribution, some of these parasite species are evolutionarily very old, raising the possibility that cospeciation explains the association between perch and these parasites.

The historical basis of an association between taxa is ultimately tied to the origin of the taxa involved. A requirement for the study of the historical ecology of an association between or among taxa is (1) an estimate of the phylogeny(s) for the taxa being considered, (2) their ancestral origins and (3) a geographic history of the areas involved (Brooks and McLennan, 1991). This information is necessary to determine if the predictable association between some parasite species and yellow perch in North America is due to ecological factors or cospeciation between the host and parasite taxa. The purpose of this chapter is to examine the historical ecology of *Perca*

flavescens in North America and its predictable parasites to determine if there is an evolutionary basis to the associations between yellow perch, its geographical distributions and its parasites. Results are interpreted to determine if the parasite fauna in yellow perch results from species maintained during invasion from elsewhere (i.e., yellow perch speciated and dispersed from elsewhere and carried the ancestral parasites along), parasites were acquired subsequent to invasion from elsewhere (i.e., yellow perch speciated and dispersed from elsewhere and picks up local parasites), or does it represent a fauna that developed *in situ* with yellow perch (i.e., yellow perch and their parasites are ancestrally associated with North America and their association is a result of this biogeographic ancestral sympatry).

METHODS AND MATERIALS

Percidae Phylogenetic Relationships

The basis for discussion for the phylogenetic hypothesis for the family Percidae (Figure 6) is from a cladistic analysis of osteologic and myologic characters (Wiley, 1992). Additional sources of information defining relationships within *Perca* and other Percidae genera come from Bodaly et al. (1989), Leary and Booke (1982), Shcherbukha (1993), Svetovidov and Dorofeeva (1963) and Todd and Hatcher (1993).

Parasite Phylogenetic Relationships

Hypotheses of relationships in the digenean subfamily Bunoderinae have been developed by Caira (1989), Brooks (1992) and Brooks and McLennan (1993). Discussion of relationships in this clade is based on the hypothesis presented by Brooks and McLennan (1993) (Figure 7).

Although the genus *Urocleidus* was shown to be polyphyletic by Beverley-Burton and Klassen (1990), they did demonstrate the clade containing *Urocleidus adspectus* to be monophyletic (Figure 8) and this will be the basis of discussions on this group of parasites. Host specificity is defined here as a parasite that reproduces only in association with one host species.

I developed a phylogenetic hypothesis for species in the nematode genus *Dichelyne* (Appendix 2) and this will be used for discussion of relationships in this group of parasites (Figure 9).

Despite extensive work clarifying the taxonomy of the genus *Proteocephalus* (Scholz, 1999), there are no published results of a cladistic analysis for proteocephalids parasitizing perch and other Holarctic freshwater fishes. Eight nominal species in the genus *Proteocephalus* were analyzed using five presumed homologous characters derived from adult morphology (Table 23). Character data were obtained by examination of museum specimens obtained from the U.S. National Museum Helminthological Collection, Beltsville, Maryland (USNPC) and reference to the literature. Character polarity was determined by outgroup analysis by reference to the plesiomorphic character states identified by Rego et al., 1998 and using species of the family Monticellidae as an outgroup (Brooks et al., 1991). Characters unshared with the outgroup were polarized using functional outgroups subsequent to preliminary resolution of ingroup relationships (Watrous and Wheeler, 1981). Characters were analyzed using the computer program PAUP 3.1 (Swofford, 1991). Multistate character transformation series that could not be ordered *a priori* were analyzed using the unordered states option in PAUP and the PAUP options mulpars, branch

and bound, and global branch swapping were used. Farris optimization (Farris, 1970) was used to determine the fit of each character transformation series.

The following characters and their states were analyzed to develop a hypothesis of phylogeny of species in the cestode genus *Proteocephalus*.

1. Apical sucker. The presence or absence of an apical sucker is an important diagnostic trait for many species of *Proteocephalus*. Two states are recognized, present or absent. Monticellidae do not have an apical organ on the scolex and accordingly the absence is considered plesiomorphic.

2. Vaginal sphincter. Two states are recognized, present or absent. Rego et al. (1998) have shown the plesiomorphic condition for proteocephalideans to be vaginal sphincter present. Accordingly, the plesiomorphic state is vaginal sphincter present.

3. Position of vaginal opening. Two states are recognized. Vaginal opening anterior to the cirrus pouch opening or vaginal opening posterior to cirrus pouch opening. Species of Monticellidae have a vaginal opening posterior to cirrus pouch opening indicating the posterior opening is plesiomorphic.

4. Vaginal canal. In some *Proteocephalus* species the vaginal canal crosses the proximal portion of the cirrus sac, while in other species it circumvents the cirrus sac to lie anterior. In the Monticellidae the route of the vaginal

canal is posterior to the cirrus sac and as a consequence there is no opportunity for the canal to cross, or circumvent, the cirrus sac. Accordingly, there are two apomorphic states for this character, neither of which are shared with the outgroup. Unordered analysis of these character states is consistent with the hypothesis that the state of the vaginal canal crossing the cirrus sac is plesiomorphic.

5. Maximum body size. Two states are recognized. The plesiomorphic state is maximum strobila length less than 75mm. The apomorphic state is considered to be maximum strobila length greater than 75mm.

Palaeontology and the Fossil Record

Sources for palaeontological information regarding the fossil record of *Perca* (Smith, 1954, 1958, 1962, 1963; Ossian, 1973; Skompski, 1977; Mein et al., 1983; Paunovic, 1984, Cavender, 1986; Carroll, 1988; Craig, 1987; Micklich and Gaudant, 1989; Nazarkin, 1993) will be discussed in relation to hypotheses proposed for the origin and present distribution of Percidae, in particular species in the genus *Perca*. Many fossils have been assigned to the family Percidae that, on more rigorous examination, have been shown to belong in other taxa. Cavender (1986) described a series of nine derived morphological characters and argued that any fossil must have at least some of these characters in order to be considered for placement in the family

Percidae. Wiley (1992) identified two synapomorphies defining the family Percidae; a single supraneural bone and a reduced number of anal fin spines from three to either two or one. Fossils must have at minimum the two synapomorphies identified by Wiley (1992) to be considered as fossil Percidae.

Palaeogeography and Plate Tectonics

The current distribution of species in the family Percidae has been explained either by a widespread ancestral distribution that has been disrupted by vicariance (Wiley, 1992), or a restricted ancestral distribution followed by dispersal into areas previously unoccupied resulting in disjunct extant distributions (Collette and Banarescu, 1977; Crossman and McAllister, 1986). In order to assess these competing views, continental palaeogeography involving the Laurasian landmass since the mid-Cretaceous is presented to identify possible routes and barriers to dispersal and vicariant events. Consideration is limited to Laurasia since there is no evidence to suggest Percidae has ever naturally existed outside of Laurasia and its derivatives. Sources for palaeogeographic information include Biske and Baranova (1976), Adams (1981), Howarth (1981), Pomerol (1982), Crossman and McAllister (1986) Carroll (1988) Dawson (1992), Rogers (1993), and Smith et al. (1994).

RESULTS

Phylogenetic Relationships

The phylogenetic hypothesis for the family Percidae (Wiley, 1992) supports the interpretation that the genus *Perca* is sister to the other genera in the family and that the family, and *Perca* is Laurasian in origin (Wiley, 1992) (Figure 6). Furthermore, *Crystallaria* and *Etheostoma* evolved in North America, and their presence in North America is not a consequence of dispersal from an ancestral location elsewhere.

There are three species recognized within the genus *Perca*: *P. flavescens* is endemic to North America, *P. fluviatilis* is endemic to Eurasia and *P. schrenki* Kessler is allopatric with *P. fluviatilis* and is restricted to the Balkhash and Alakul' lakes drainage in eastern Kazakhstan (Craig, 1987). *Perca flavescens* and *P. fluviatilis* are considered sister species (Collette and Banarescu, 1977; Shcherbukha, 1993).

Parasite phylogenies

The hypothesis of phylogeny shown in Figure 7 supports the interpretation that the digeneans *C. cooperi* and *B. luciopercae* have a Laurasian distribution and origin. The placement of *B. luciopercae* relative to other species in this subfamily is, at present, unclear but its presence in North America and Eurasia is an indication that this parasite is at least

Laurasian in age and provides no evidence for cospeciation with *P. fluviatilis* in Eurasia or *P. flavescens* in North America. *Crepidostomum cooperi* is endemic to North America and is reported from many host species. It forms an unresolved monophyletic clade (Brooks and McLennan, 1993) with *C. cornutum* (Osborn, 1903), a parasite normally associated with North American endemic centrarchids, and *C. ictaluri* (Surber, 1928) a parasite usually associated with North American endemic ictalurids. Because of this close relationship with North American endemic species, it is reasonable to assume that *C. cooperi* is derived from a North American ancestor and these three parasite species all are shared among hosts whose ranges and biology overlap.

The gill monogenean *U. adspectus* is the only parasite exhibiting strict host specificity for yellow perch. This parasite is one of four species of uncertain relationships within the subfamily Ancyrocephalinae (Figure 8) (Beverley-Burton and Klassen, 1990). The ancestral host-association in this subfamily is with fishes in the families Centrarchidae and Moronidae. Subsequently the association with Moronidae was lost and there was ecological diversification into several different host families (Figure 8) due to host switching. Although relationships within the clade containing *U. adspectus* are unresolved, it is monophyletic, each of the species is

associated with hosts belonging to three different host families and it is sister to *Ligictaluridus*, a group parasitizing ictalurid catfishes.

The genus *Dichelyne* is monophyletic (Appendix 2) and this phylogenetic hypothesis supports the interpretation that species of *Dichelyne* present in fish hosts from North American form a monophyletic clade that is apomorphic relative to species present in South American and Pacific hosts. This hypothesis (Appendix 2) does not support cospeciation to explain the predictable association between *Dichelyne cotylophora* and *P. flavescens*. That this association results from a host switch into perch, and other hosts, by this nematode species, is the most parsimonious explanation.

Phylogenetic analysis of *Proteocephalus* species resulted in one tree five steps long (Figure 10) with a consistency index of 100%. This hypothesis of phylogeny proposes that *Proteocephalus percae* and *P. longicollis* (Zeder, 1800) form an unresolved polytomy that is sister to the remaining species. Of these remaining taxa, *Proteocephalus fillicollis* Rudolphi, 1802 and *P. pearsei* are sister taxa, *P. ambloplitis* (Leidy, 1887) and *P. stizostethi* are sister taxa and these four species form an unresolved polytomy with *P. macrocephalus* (Creplin, 1875) and *P. pinguis* La Rue, 1911. The widespread distribution of species in this genus (Yamaguti, 1961) is an indication of an origin at least as far back as Laurasia and likely much

older. This hypothesis does not support a sister-species relationship between *P. pearsei* and *P. percae* and does not support a cospeciation explanation for the association between these two cestode species and their respective perch hosts.

Palaeontology and the Fossil Record

The fossil record of *P. flavescens* in North America begins in the mid-Pleistocene (Smith, 1958, 1962; Cavender 1986; Carroll, 1988; Craig, 1987) with deposits located in Kansas (Smith, 1958, 1963), Nebraska and Oklahoma (Smith, 1954, 1958), Texas (Semken, 1966) and South Dakota (Ossian, 1973). The earliest *P. fluviatilis* fossil in Europe is dated to the Miocene (26 mybp) in the Crimea (Lebedev, 1952) and France (Mein et al., 1983). Fossil *Perca* dating to the Pliocene (6 mybp) are reported from Austria (Weinfurter, 1950) and Belgium (Newton, 1908) and from the Pleistocene deposits from eastern Siberia (Svetovidov and Dorofeeva, 1963; Nazarkin, 1993) to many sites in Europe (e.g. Weiler, 1933; Grippe and Beyle, 1937; Skompski, 1977; Paunovic, 1984; Lister et al., 1990).

Fossils belonging to the genus *Mioplosus* are reported in Eocene deposits collected from the Green River formation of western Wyoming (Thorpe, 1938). These are considered to belong in the family Percidae, but have just two of the traits identified by Cavender (1986). *Mioplosus* has a

reduced number of anal spines but has three supraneurals. This fails to meet the minimum number of synapomorphies I have set for inclusion in Percidae and at present, I do not consider *Mioplosus* to belong in this family. However, it may well represent a form ancestral to this family.

Palaeogeography and Plate Tectonics

During the mid Cretaceous (105 mybp [= million years before present]) North America was divided from north to south by a marine incursion and was connected to Greenland and Europe in the east and to Siberia in the west (Smith et al., 1994) (Figure 11). The western cordillera orogeny was widespread from northern Alaska to Mexico (Rogers, 1993). Present day Europe and Asia were separated by penetration of the Obik Sea from the north and this separation was complete by 95 mybp. In Europe, the Alps were beginning to form and western Europe was a group of islands with some other large islands in the present day Caspian-Aral Sea basin. In the north, Scandinavia was connected to northern Russia. The result was a Siberian-western North American landmass and a western European-eastern North American landmass. This general configuration was maintained in varying degrees until 70 mybp.

During the Palaeocene (63mybp-60 mybp), the western cordillera was well formed in North America and the inland continental sea receded to

rejoin the western and eastern halves of the continent. North America was connected to Europe through Greenland and the Faroe Islands in the east and to Siberia across the Bering Strait in the west. Europe was separated from Asia by the Obik Sea (Figure 12).

The connection between Europe and North America across the North Atlantic was beginning to separate during the Eocene (53 mybp - 37 mybp) (Gentry and Sutcliffe, 1984; Rogers, 1993) while Europe and Asia were still divided by the Obik Sea (Adams, 1984). Europe and Asia were contiguous only by the Oligocene (30 mybp) with the disappearance of the Obik Sea. (Adams, 1984) (Figure 13).

During the Miocene (20 mybp - 10 mybp), North America was connected to Siberia in the west and Greenland in the east and the connection to Europe, across the North Atlantic (Smith et al., 1994) (Figure 14). In Europe there were many peninsulas and islands projecting into the Paratethys Sea from the west, an area congruent with the present day western basin of the Black Sea. By the mid-Miocene, the Paratethys has divided into 3 major basins containing many large islands. The westernmost basin became isolated and brackish, followed in sequence by the central and eastern basins. By the mid-late Miocene, these three basins were entirely

freshwater and corresponded to the present day Prut, Dniestr, Danube watersheds.

The scenario of increasing separation between North America and Europe with the continued opening of the north Atlantic and the drying of the inland sea in Europe lead to the present day configuration. There has been continued connection and disjunction between Siberia and Alaska across the Bering Strait associated with climatic events, especially Pleistocene glaciations.

DISCUSSION

The question of the origin of an association between or among taxa is inevitably tied to the origin of the taxa themselves. The origin of the association between yellow perch and a predictable suite of parasites in North America must therefore account for the origin of the taxa in question.

Different hypotheses have been proposed to explain the origin of *Perca* in North America. One view is that *Perca* (and *Stizostedion*) moved east from Europe into Siberia and from there dispersed into North America over Beringia during the Pleistocene (McPhail and Lindsey, 1970; Collette and Banarescu, 1977) placing *Perca* (and *Stizostedion*) in North America no earlier than 1.5 mybp. This I will call the Beringia dispersal hypothesis (BDH). An alternate hypothesis has *Perca* or its ancestor migrating into North America from Europe by way of a North Atlantic land bridge (Balon et al., 1977). Interestingly, this is the route Collette and Banarescu (1977) proposed for the arrival of Etheostomatini in North America during the Eocene (~50 mybp). This I will call the North Atlantic dispersal hypothesis (NADH). A third hypothesis is that Percidae is a Laurasian clade that dates to the early Tertiary about 65 mybp (Wiley, 1992). This I will call the Laurasian origin hypothesis (LOH).

There are two caveats relevant to the discussion of the fossil record of Percidae in general and *Perca* in North America in particular. First is the incomplete nature of the fossil record. Between the late Cretaceous and Pleistocene, virtually all the fossil deposits containing freshwater fishes in North America are located along the western continental divide, an area outside of the known distribution of yellow perch. Second is the recognition of fossilized specimens as members of the family Percidae, or the genus *Perca*. Many species placed in Percidae have, on subsequent examination, been shown to be incorrectly assigned.

The BDH depends on *Perca* being present in eastern Siberia during the Pleistocene. Supporting this are Pleistocene deposits containing fossil *Perca* in Siberia (Nazarkin, 1993) that extend beyond the current distribution of *P. fluviatilis*. However, the presence in North America of Pleistocene *P. flavescens* fossils in areas far south of the southern extent of the Pleistocene glaciers is a clear indication that perch were in North America prior to the Pleistocene. The interpretation that perch used the Beringian landbridge as a dispersal route appears to stem from three sources. First, the oldest *Perca* fossil is European; second, it assumes a dispersalist paradigm that predates our knowledge of plate tectonics and third, the only connection between North America was across the Bering land bridge exposed during

Pleistocene glaciation. This information led to the assertion that perch originated in Europe and that the only route for dispersal into North America was via Beringia. However, while Beringia did connect Siberia to North America during the Pleistocene, and during other epochs as well, there are several reasons that perch would be unable to use this as a route of dispersal. First, the glaciers themselves would present a barrier to perch dispersal. Second, perch are not strong swimmers and high rates of flow limit their distribution (Craig, 1987). The barrier presented by the western continental mountain ranges and the high velocity water flow associated with streams and rivers in that region would prevent perch dispersal. Thus the current data do not support BDH.

The NADH and the LOH both require that *Perca* be at least as old as the Eocene (53 mybp - 37 mybp) when North America and Europe were still connected across the North Atlantic. This connection was maintained until the early Oligocene (30 mybp). Europe was separated from Siberia by the Obik Sea through the Eocene and this separation remained until the Oligocene (30 mybp) when the Obik Sea receded. The earliest *Perca* fossil in western Europe is from Miocene deposits (26 mybp) in the Crimea and France and in Siberia from Pleistocene deposits, thus *Perca* originated west of the Obik Sea and dispersed eastward after the Obik Sea receded. This

would support the interpretation that *Perca* existed in western Europe at a time when there was a connection between Europe and North America and Europe and Siberia were separated.

Support for an older age for *Perca* than indicated by the fossil record comes from consideration of the origins of the European genera *Gymnocephalus*, *Stizostedion*, and *Romanichthyes.* The Paratethys occupied distinct basins, each with a unique history, as they disappeared during the Miocene. Many of these basins are represented today by the Black Sea drainages including the Prut, Dniestr, Danube watersheds. This area currently has the most species of *Gymnocephalus*, *Stizostedion*, and *Romanichthyes*. Vicariant events associated with the drying of the Tethys and Paratethys were the probable cause of speciation in these Percidae genera and lends credence to a much older age for Percidae than indicated solely by the fossil record. If this vicariant event is an explanation for the existence of *Gymnocephalus*, *Stizostedion*, and *Romanichthyes* in Europe, then *Perca*, as sister taxon to the other genera in the family, would predate the Miocene. Furthermore, it is likely that *Stizostedion* also predates the Miocene and has a Laurasian origin.

Fossils of *Mioplosus* appear to provide additional evidence on the age and origin of *Perca. Mioplosus* species are reported from the Eocene Green

River deposits of western Wyoming. Although these fossils do not meet all the criteria I have set for inclusion in Percidae they are frequently considered to belong in Percidae (Carroll, 1988) and may represent an ancestor to the Percidae. If this supposition is correct, there would be fossil evidence of a percid ancestor in North America during the Eocene (60 - 40 mybp).

The hypothesis of phylogeny for Percidae proposed by Wiley (1992) has the ancestor of Percidae occurring in both North America and Eurasia and is consistent with a Laurasian origin for Percidae. The disjunct distribution in both North America and Eurasia of the genera *Perca* and *Stizostedion* can be interpreted as a result of dispersal from the ancestral area followed by speciation due to vicariance. The vicariant event would be the separation of Europe from North America due to the opening of the North Atlantic. I cannot, using the fossil and phylogenetic data for the percids alone, choose between LOH and the NADH.

Since there is no fossil record for parasites in this study, I must rely on inferences drawn from phylogenetic hypotheses as they relate to host and geographic associations. The digenean subfamily Bunoderinae is Holarctic in distribution and is associated with the Salmoniformes, Centrarchidae and Percidae fish taxa. From the distribution of species in this subfamily, it is at least Laurasian in origin. Two species in the subfamily have been identified

as associating predictably with *Perca* hosts. *Crepidostomum cooperi*, endemic to North America, is predictably associated with yellow perch in North America and *B. luciopercae*, with a Holarctic distribution, is predictably associated with perch in Eurasia (Carney and Dick, 1999). The host species for the sister taxa of *C. cooperi* are centrarchids and ictalurids, both endemic to North America, suggesting an ancient association. Lack of host specificity by *C. cooperi* (see Caira, 1989) and ecological overlap with these other host species is consistent with a host switch explaining how this parasite acquired *P. flavescens* as a host. The origin of the association between *B. luciopercae* and perch in Eurasia is less clear. *Bunodera luciopercae* is Holarctic, and has been reported from numerous host species on both continents including yellow perch in North America. The distribution of *B. luciopercae* could represent a Laurasian origin and its apparent preference for percids is an indication that this association is also old.

Urocleidus adspectus is the only parasite specific for *P. flavescens*, but this association results from host switching from a lineage originally associated with centrarchids rather than cospeciation (Figure 2). The ancestral hosts in North America are centrarchids and the sister group to the clade containing *U. adspectus* is associated with ictalurid catfish. The

earliest fossil centrarchids are recorded from the Eocene (55 - 35 mybp) and fossil ictalurids are known from the Paleocene (65 mybp) and it is possible that this group of parasites dates to the same time period as the hosts for which they are specific.

The phylogenetic hypothesis for *Dichelyne* species (Appendix 2) supports the interpretation that those species in South America and in the Pacific are ancestral, relative to those in North American waters, and that the species present in North America constitute a monophyletic lineage evidence of a single dispersal into North America. The presence of *Dichelyne* in North America, India, the Pacific and North America supports an ancient origin for these parasites. The association of *D. cotylophora* with *P. flavescens* is best explained by a host switch. It is worth noting that *D. cotylophora* is the sister taxon to *D. lepisosteus* which is associated with gars, a fish family known from the early Cretaceous (135 mybp).

Distinguishing among *Proteocephalus* species has been based on a restricted set of morphological traits that have been shown to be insufficient (Hanzelova et al., 1994; 1995). Furthermore, a large number of previously recognized species have been synonymized and are considered to be morphologically highly polymorphic, being affected by host, age, geography and other influences (Hanzelova and Scholz, 1999; Scholz and Hanzelova,

1994; 1999). Nonetheless, Hanzelova and Scholz (1999) were able to identify morphological traits that reliably distinguished among taxa, in particular the presence of a vaginal sphincter and the course of the vaginal canal. To these I have added the presence of an apical sucker, the position of the vaginal pore relative to the cirral pore and the overall maximum body size. While this list of reliable characters is short, it has permitted a degree of resolution of relationships for the species considered that is sufficient to answer the question of whether *Proteocephalus pearsei* and *Proteocephalus percae* are sister species.

If there is cospeciation between *Perca flavescens* and *Proteocephalus pearsei* in North America or *Perca fluviatilis* and *Proteocephalus percae* in Eurasia, then the two cestode species should be sister taxa. The hypothesis of phylogeny presented for the species examined in this analysis does not support a sister taxa relationship between these two species and as a consequence does not support cospeciation as the basis for the association between *P. pearsei* and yellow perch. The presence of *Proteocephalus pearsei* in yellow perch is best explained by host switching. Similarly, *Proteocephalus percae* in the perch in Eurasia is best explained by host switching. *Proteocephalus* as a group is Holarctic suggesting a Laurasian origin. Furthermore, the host associations include Anguillidae and

Salmoniformes also indicating an ancient origin for these cestode species and their host associations. It is worth noting that *Proteocephalus stizostethi* Hunter and Bangham, 1932 and *Proteocephalus pearsei*, both associated with hosts from different genera in the family Percidae, also are not sister taxa, providing additional evidence for the absence of coevolution as an explanation for host-parasite associations within this genus, at least for the species I examined.

In Chapter 1, I recorded predictable associations between some parasite species in yellow perch in North America and perch in Eurasia and proposed that the basis for these associations was ecological, and not cospeciation (Carney and Dick, 1999). The central question to this chapter was the origin of the associations between those predictable parasites and yellow perch in North America. Taking into account the host phylogeny, fossil record and parasite phylogenies, the following interpretations can be made. *Perca flavescens* and the other taxa in the family Percidae are much older than the fossil record indicates. The presence of *P. flavescens* in North America, and the disjunction with *P. fluviatilis* in Eurasia, is a consequence of a North America-Europe ancestral distribution that was severed with the opening of the North Atlantic, and dispersal of *P. fluviatilis* from Europe into Asia after the Obik Sea disappeared. The association between *P.*

flavescens and its suite of predictable parasites developed *in situ* as a result of switching from ecologically sympatric hosts, especially the North American endemic Centrarchidae and Ictaluridae. The association of *C. cooperi*, and *U. adspectus* with *P. flavescens* is best explained by a host switch from either North American endemic ictalurids or centrarchids. The immediate sister taxa to *P. pearsei* are found in North American salmonids and centrarchids (Figure 5) suggesting the importance of centrarchids as a source of parasites for yellow perch in North America. A host switch is the best explanation for the origin of the association between *D. cotylophora* and *P. flavescens* but the ancestral host is still unknown.

In summary, the parasite data support an interpretation that host switching from North American endemic hosts was the source of the parasites which are predictably associated with yellow perch in North America and the basis for this host switching is ecological. With the exception of *U. adspectus*, these parasites are characterized by a lack of host specificity, suggesting these non-host specific parasites make use of host ecological "relatedness" rather than phylogenetic relatedness in determining their host associations. Ecological overlap allows for the acquisition of these parasites since perch, with a non-specialized ecology, acquire these non-host specific parasites through shared feeding habits. Yellow perch and its

predictable parasites evolved in North America as a result of shared geography and host switching from other sympatric host species, which have similar ecological requirements.

The preceding evidence supports the following interpretation. *Perca* had a Laurasian distribution and its extant presence in North America and in Europe represents its ancestral distribution. Speciation in many of the European genera was a consequence of vicariant events associated with the drying of the Tethys and Paratethys Seas during the Miocene. The presence of different species of *Perca* and *Stizostedion* in North America and Europe also results from vicariance, in these instances the separation of Europe and North America. There is no evidence to support the contention that either *Perca flavescens* or *Stizostedion* spp. dispersed into North America from Siberia during the Pleistocene.

Table 23. Character matrix for numerical phylogenetic analysis of 8 species in the cestode family Proteocephalidae parasitizing holarctic freshwater fishes.

Taxa	**Characters**				
	1	**2**	**3**	**4**	**5**
Outgroup*	0	0	0	0	0
P. filicollis	0	0	1	1	1
P. ambloplitis	1	0	1	1	0
P. longicollis	0	0	1	0	0
P. macrocephalus	0	0	1	1	0
P. pearsei	0	1	1	1	1
P. percae	0	0	1	0	0
P. pinguis	0	0	1	1	0
P. stizostethi	1	0	1	1	0

*Outgroup is a composite, based on outgroup comparisons of several taxa, used to facilitate computer analysis.

Figure 6. Hypothesis of phylogeny for the family Percidae proposed by Wiley (1992). Current zoogeographic affinities for each genus mapped on to the cladogram.

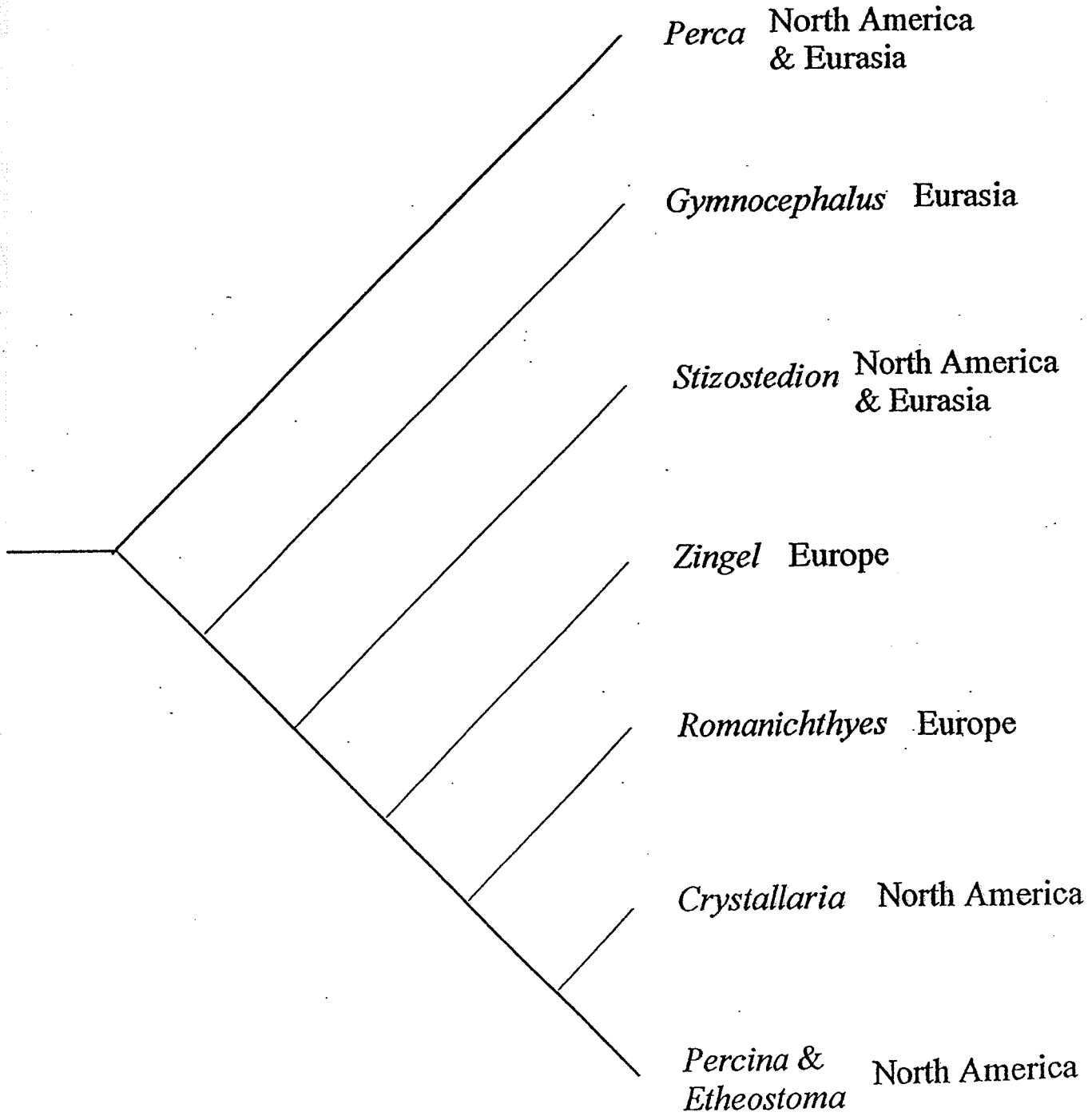

Perca North America & Eurasia
Gymnocephalus Eurasia
Stizostedion North America & Eurasia
Zingel Europe
Romanichthyes Europe
Crystallaria North America
Percina & *Etheostoma* North America

Figure 7. Hypothesis of phylogeny for species of Bunoderinae. Redrawn from Brooks and McLennan (1993). Geographic affinities and host associations are mapped on to the cladogram.

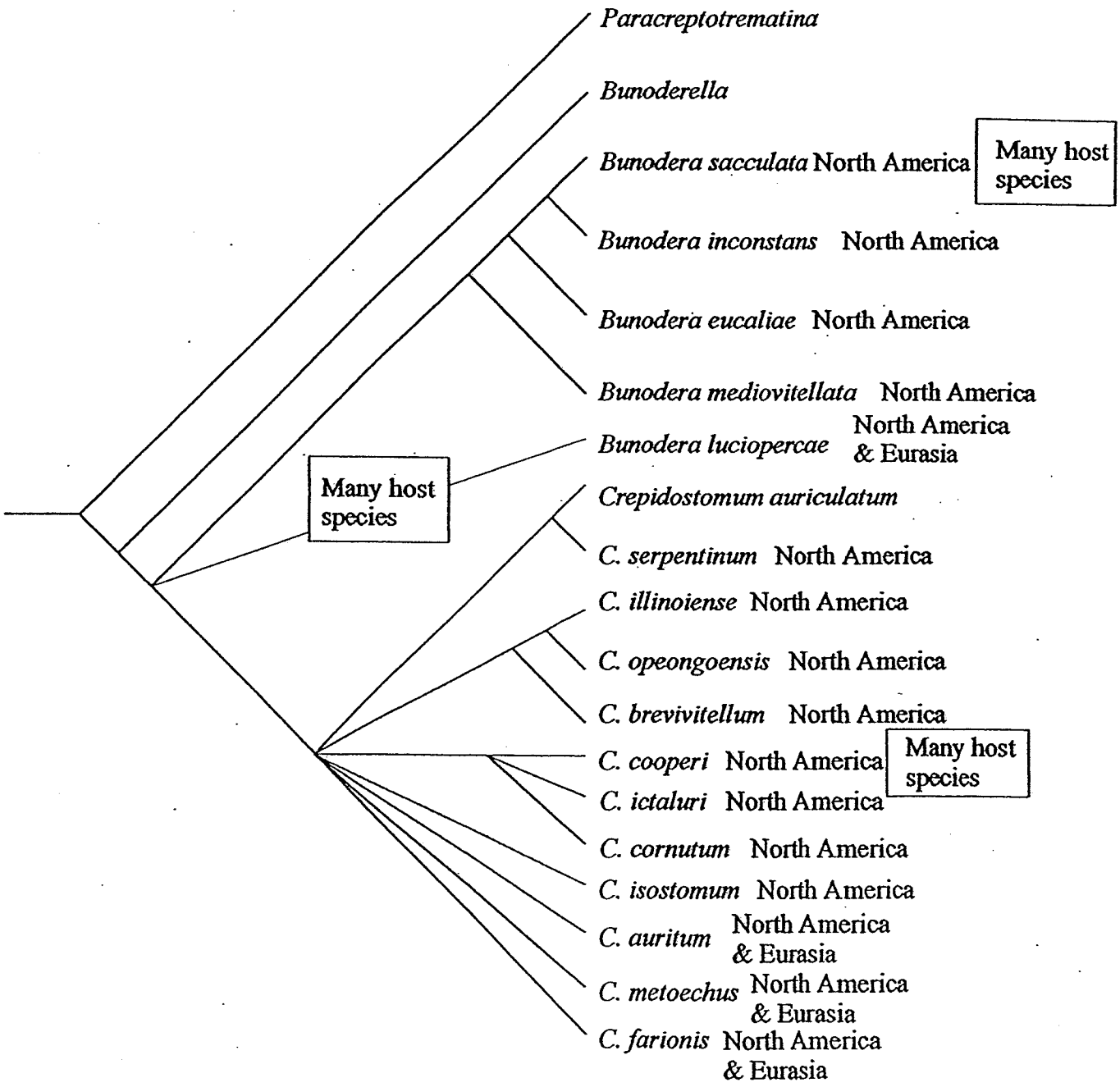
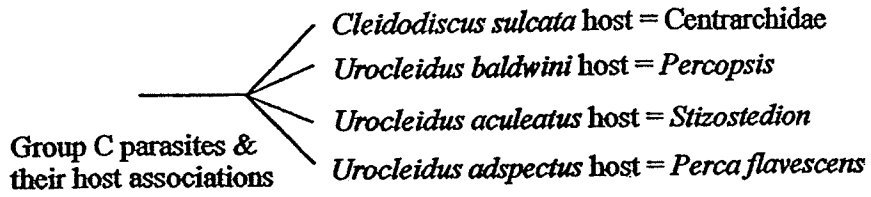

Paracreptotrematina
Bunoderella
Bunodera sacculata North America
Many host species
Bunodera inconstans North America
Bunodera eucaliae North America
Bunodera mediovitellata North America
Bunodera luciopercae North America & Eurasia
Many host species
Crepidostomum auriculatum
C. serpentinum North America
C. illinoiense North America
C. opeongoensis North America
C. brevivitellum North America
C. cooperi North America
C. ictaluri North America
Many host species
C. cornutum North America
C. isostomum North America
C. auritum North America & Eurasia
C. metoechus North America & Eurasia
C. farionis North America & Eurasia

Figure 8. Hypothesis of phylogeny for species of ancyrocephalid monogeneans redrawn from Beverley-Burton and Klassen (1990). Changes in host associations mapped on to thecladogram. Inset is species in Group C and their host associations


Group C parasites & their host associations
Cleidodiscus sulcata host = Centrarchidae
Urocleidus baldwini host = *Percopsis*
Urocleidus aculeatus host = *Stizostedion*
Urocleidus adspectus host = *Perca flavescens*

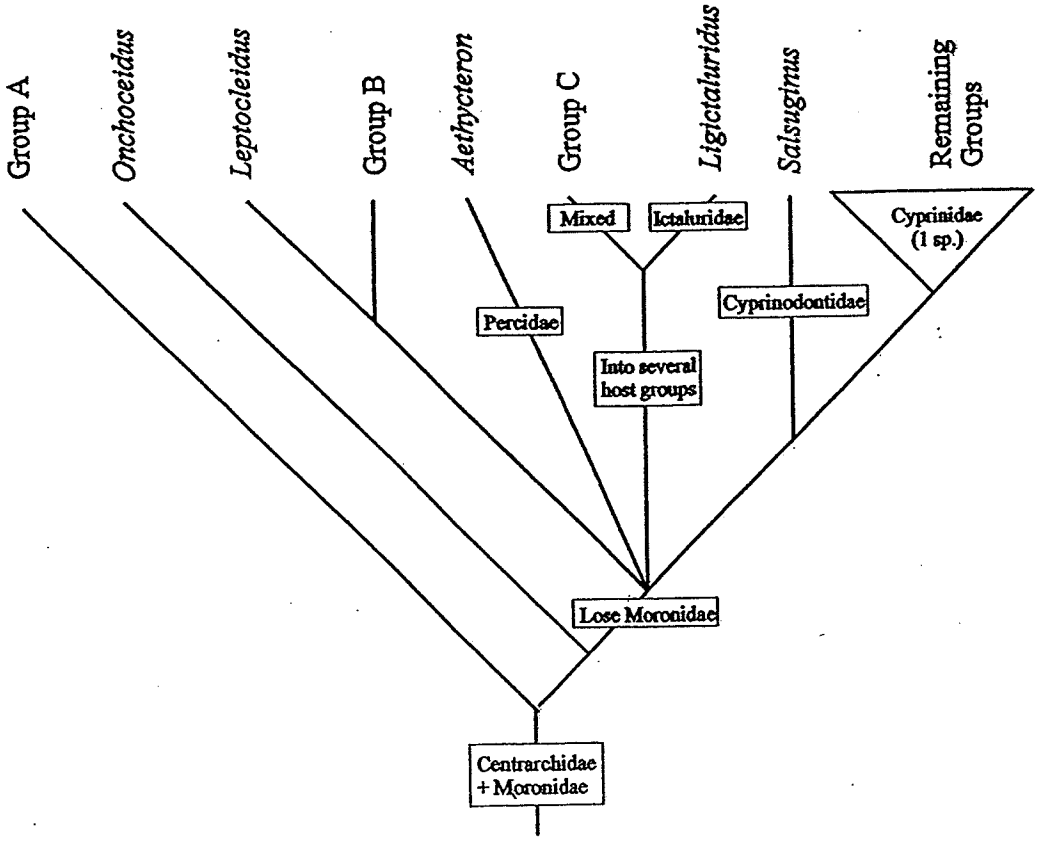

Group A
Onchocleidus
Leptocleidus
Group B
Aethycteron
Group C
Ligictaluridus
Salsuginus
Remaining Groups
Mixed
Ictaluridae
Cyprinidae (1 sp.)
Percidae
Cyprinodontidae
Into several host groups
Lose Moronidae
Centrarchidae + Moronidae

Figure 9. Hypothesis of phylogeny for species in the genus*Dichelyne* (from Appendix 2). Geographic affinities are mapped on to the cladogram

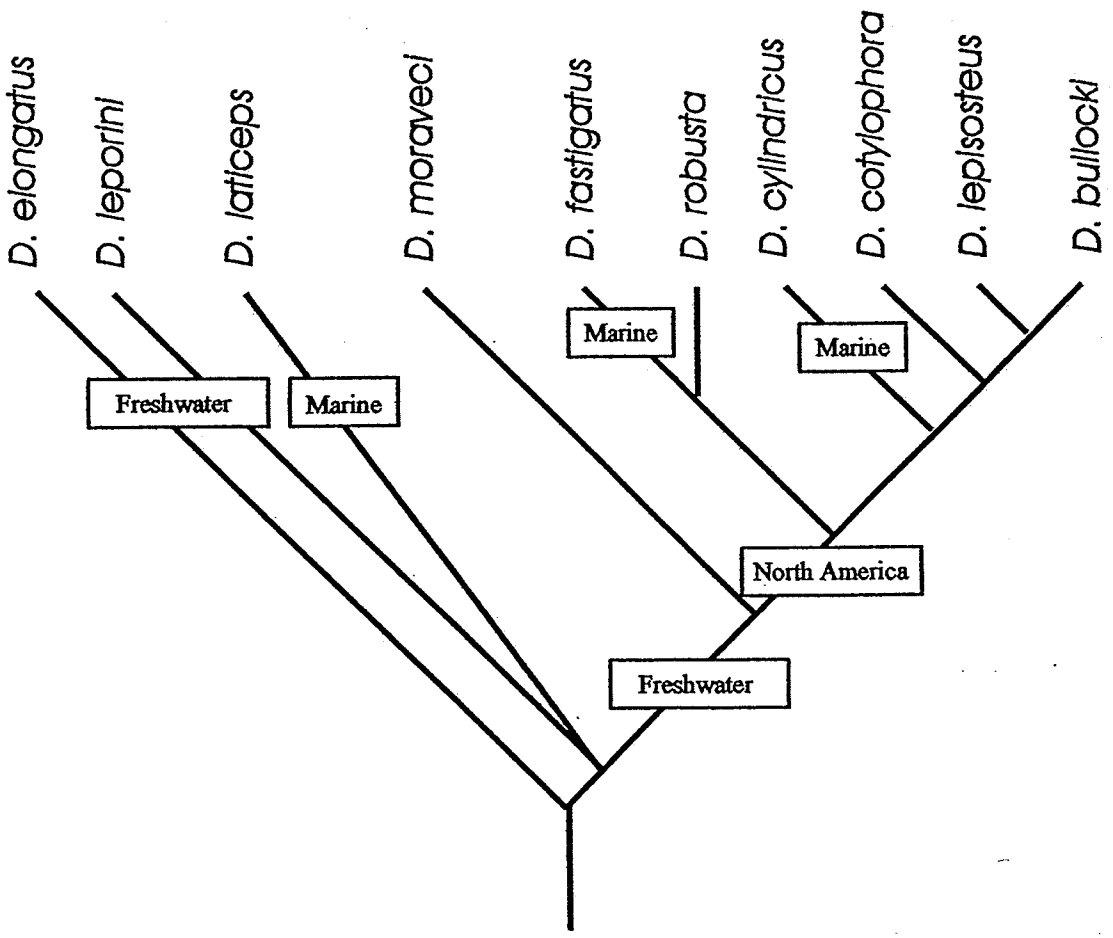

D. elongatus
D. leporini
D. laticeps
D. moravecl
D. fastigatus
D. robusta
D. cylindricus
D. cotylophora
D. leplsosteus
D. bullockl
Freshwater
Marine
Marine
Marine
North America
Freshwater

Figure 10. Hypothesis of phylogeny of some species of *Proteocephalus* based on cladistic analysis of the data matrix shown in Table 23.

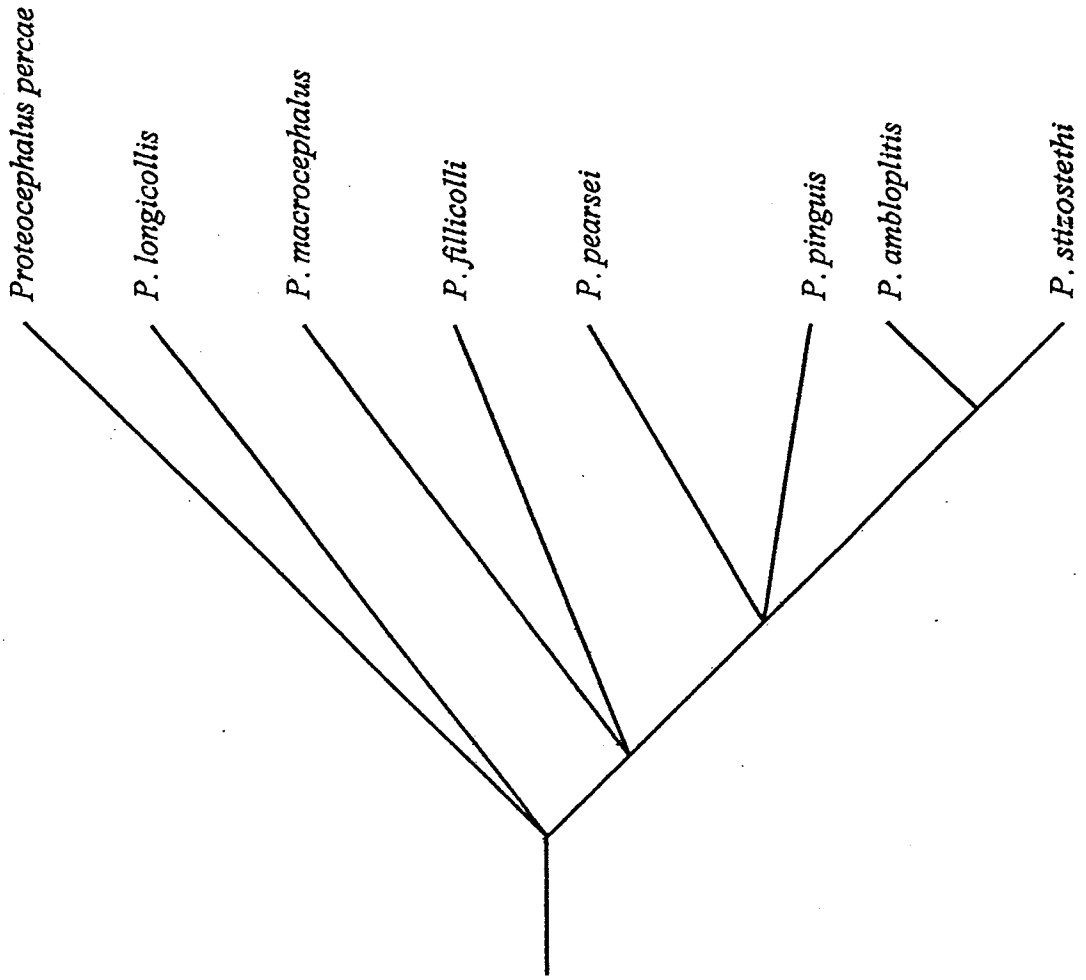

Proteocephalus percae
P. longicollis
P. macrocephalus
P. fillicolli
P. pearsei
P. pinguis
P. ambloplitis
P. stizostethi

Figure 11. Continental configurations and connections during the mid-Cretaceous (88 mybp). (Reprinted from Smith et al., [1994] with permission of Cambridge University Press).

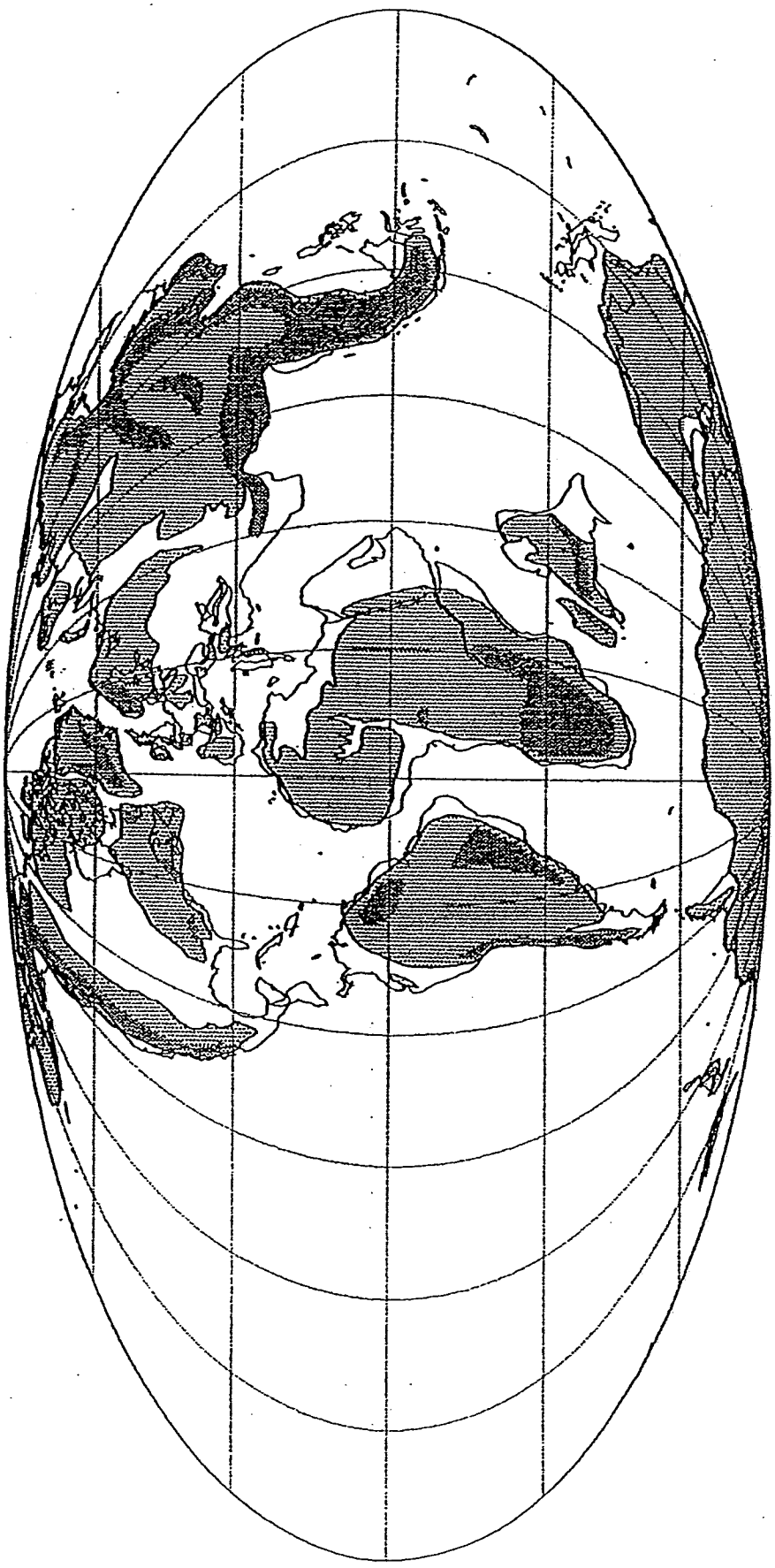


Figure 12. Continental configurations and connections during the Palaeocene (60 mybp). (Reprinted from Smith et al., [1994] with permission of Cambridge University Press).

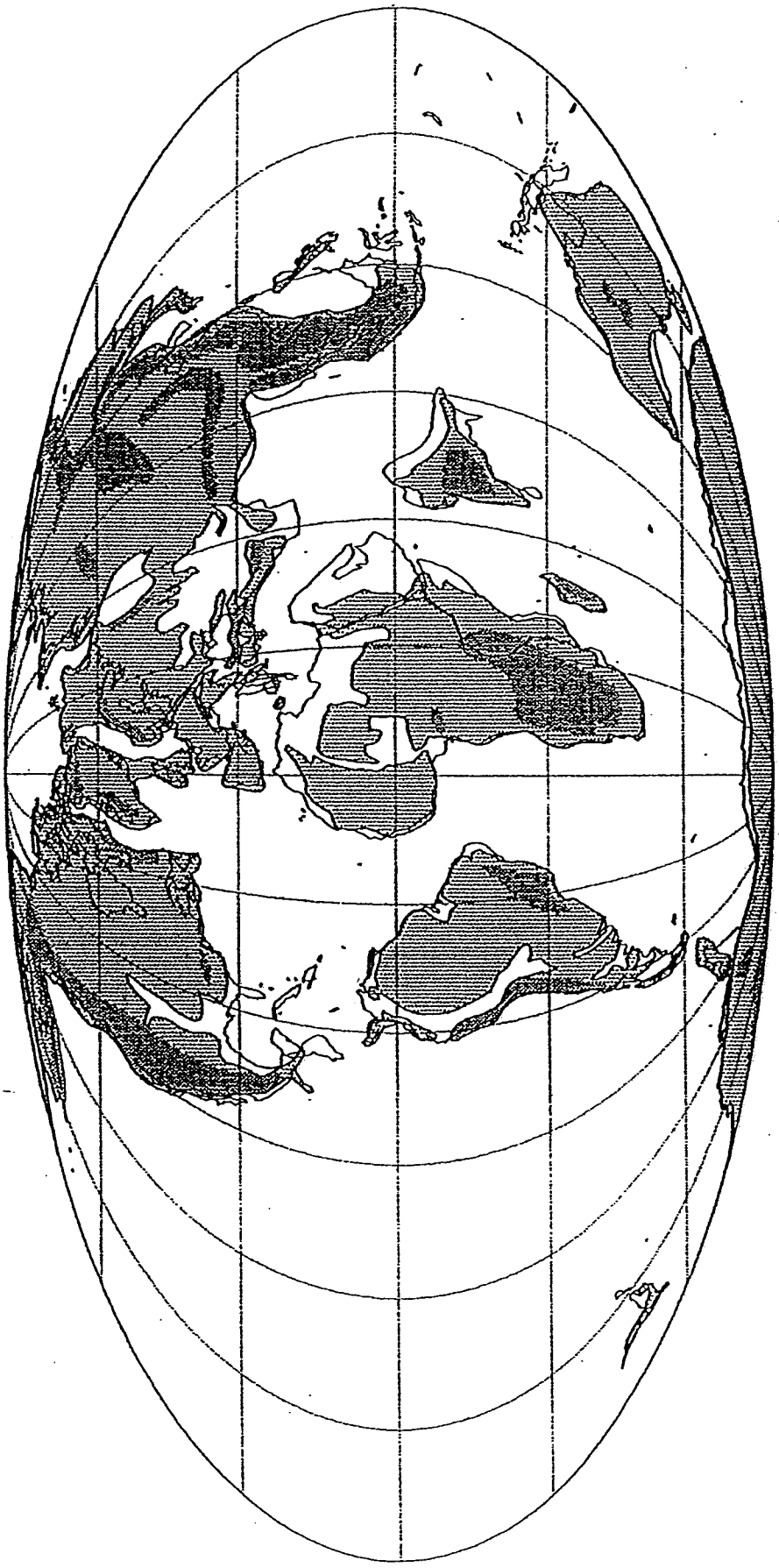
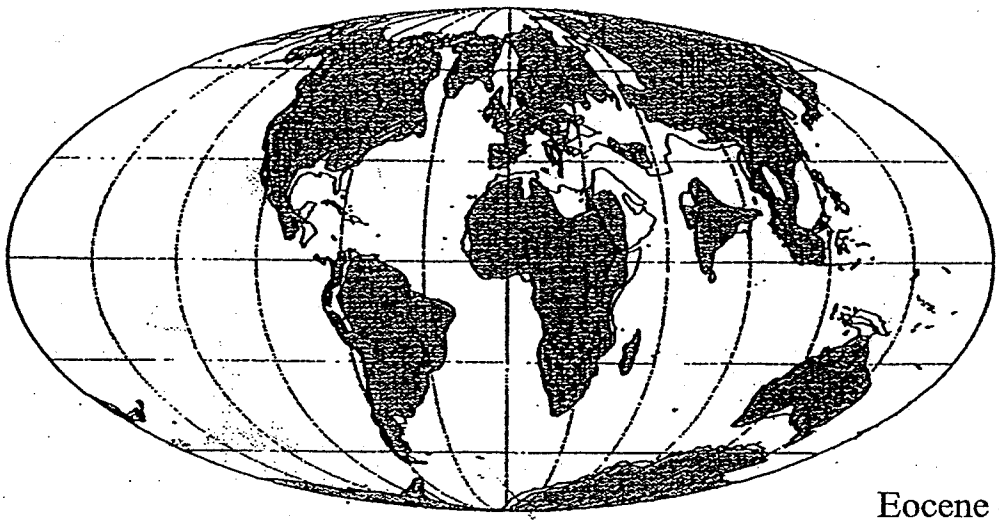
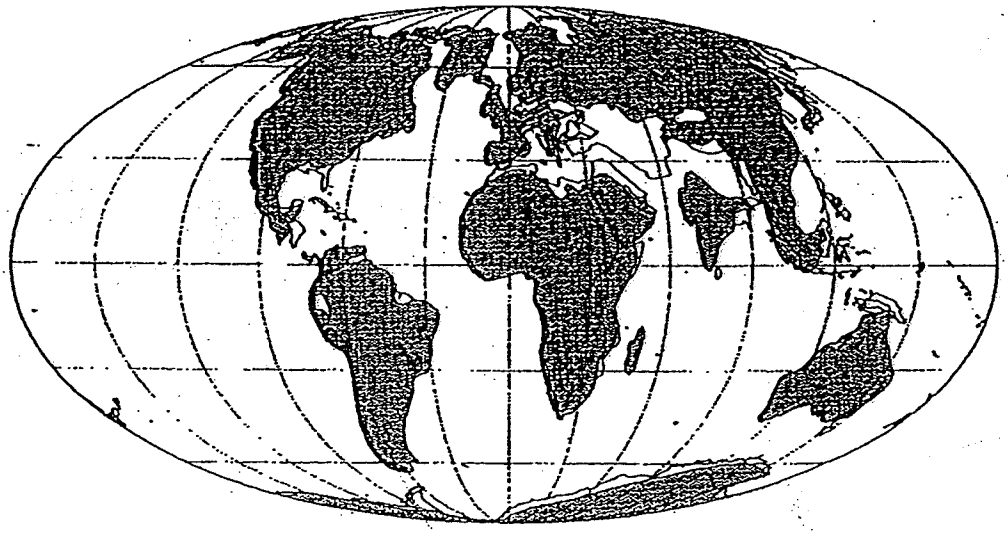


Figure 13. Continental configurations and connections during the Eocene-Oligocene (45 mybp and 30 mybp). (Reprinted from Smith et al., [1994] with permission of Cambridge University Press).

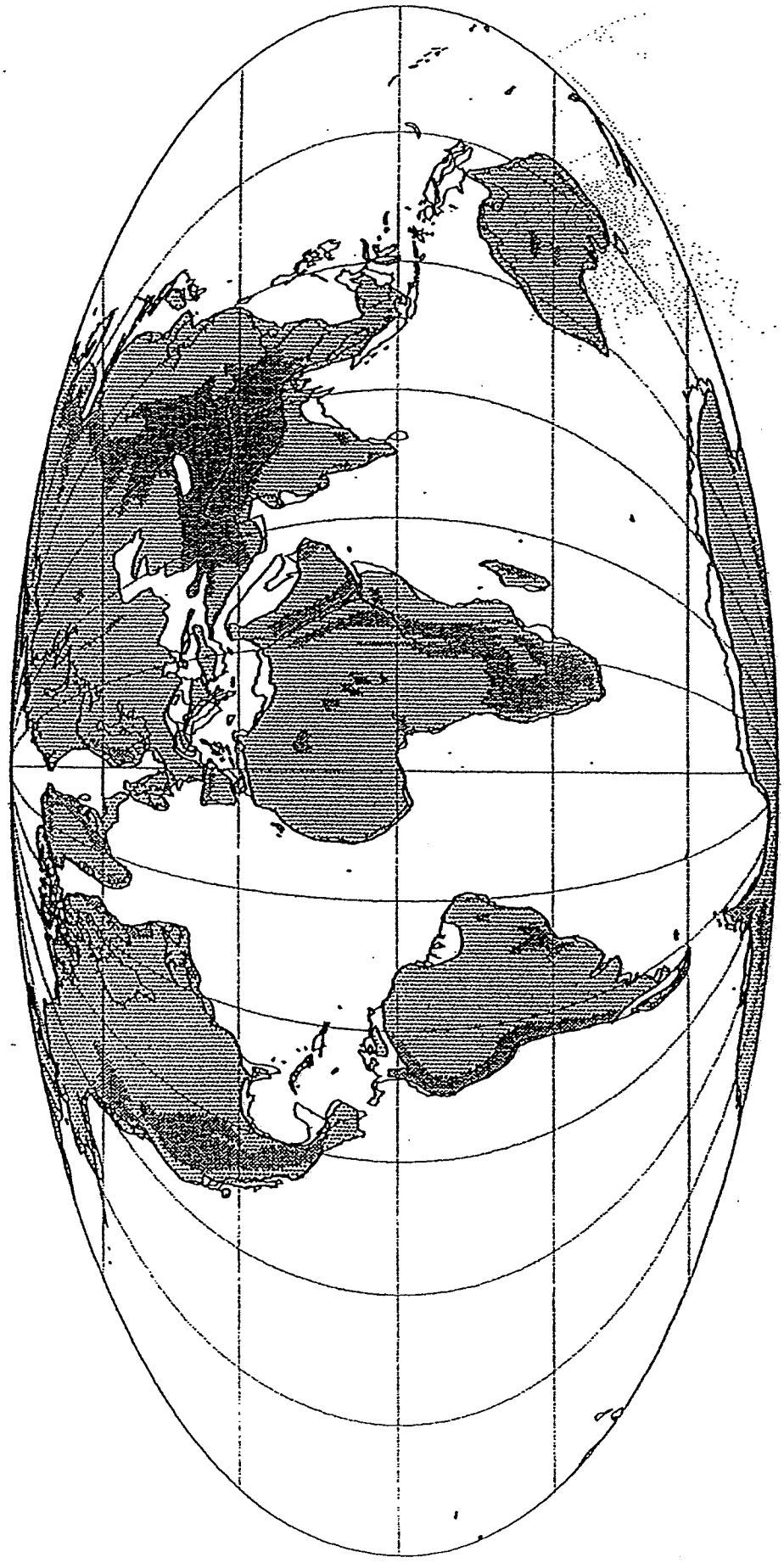


Eocene (45 mybp)



Oligocene (30 mybp)

Figure 14. Continental configurations and connections during the Miocene (20 mybp). (Reprinted from Smith et al. [1994] with permission of Cambridge University Press).



GENERAL DISCUSSION

The fundamental questions in the study of parasite communities in freshwater fish is do they have predictability or are they stochastic assemblages and what are the factors which shape those communities. Predictability in parasite communities is reported to be affected by host specificity and this may occur above a single host species, (i.e. at the host genus or family level [Choudhury and Dick, 1993, 1998]). It is less clear if there is predictability in the parasite infracommunities in the absence of host specificity. Interactions among species may be important in shaping the parasite infracommunities. Parasites that interact are predictable in the community and are often host specific (Bush and Holmes, 1986b). It has been suggested that the parasites of freshwater fishes are non-interactive (Kennedy et al., 1986) and are not predictable (Kennedy, 1990). Host specificity has often been considered to be a consequence of historical phylogenetic processes such as cospeciation and implies that predictability in the parasite communities of freshwater fish depends on phylogenetic influences. The processes structuring parasite communities are likely both ecological and phylogenetic. While most researchers realize the importance of contemporary ecological processes or historical phylogenetic influences in shaping parasite communities, there are few studies in which both

processes have been addresses in order to assess the relative importance of each.

This thesis is concerned with the patterns, processes and origins of the associations for species in the parasite communities of yellow perch in North America. Yellow perch provide an excellent model system to address these questions. The sister taxon to yellow perch is located in Europe and Asia and provides a comparison to determine if there are similarities in the composition of their respective parasite communities and if there are patterns in the parasite communities associated with the two hosts at the scale of the continent. In addition, parasites of yellow perch are, with one exception, characterized by a lack of host specificity at the host species level. Therefore, if there are repeatable patterns and processes in these parasite communities, they are not due to host specificity. Finally, yellow perch have comparatively non-specialized behaviour, habitat and feeding habitats. They are widespread and abundant in slow-flowing or lacustrine habitats in temperate regions of the northern hemisphere with their distribution being limited by temperature and water flow. They are gape-limited, feeding on a variety of food items providing a potentially wide source of food-transmitted parasites.

Yellow perch and the Eurasian perch have remarkably similar parasite communities but these are comprised of different species. Both hosts have a small group of predictable parasites that are not host specific and a large group of species that occur randomly. Observations that few of the parasites are common to both hosts were unexpected because these hosts are sister species. A substantial stochastic aspect to the parasitofauna of both hosts is demonstrated by the large number of species present at low frequency among samples. Predictability is indicated by the presence in each host of a different suite of enteric parasites present at high frequency. By modes of transmission and lack of host specificity, there is an ecological basis for the predictability of these parasites. Moreover, the parasite fauna of each host overall is as similar, and therefore as predictable, as any other biological trait shared by sister species. As sister species, these hosts have inherited similar physiology, habitat requirements, behaviour and feeding habits. As a consequence of these inherited similarities, they predictably acquire ecologically similar, but taxonomically different parasites. For hosts such as yellow perch and Eurasian perch, which are characterized by non-host specific parasites, their component communities at the continental scale are not merely stochastic assemblages but have predictable components. Furthermore, the overall pattern of parasitism is remarkably similar despite

separation for millions of years and associating with taxonomically different parasites.

Although it is a useful first step to demonstrate patterns and predictability in the parasite fauna across the continental distribution of a host species, it is interactions and processes at the comparatively fine scale of the local component and infracommunities that produce these patterns.

The patterns and predictability demonstrated at the continental scale extend also to the local component communities and infracommunities. Taxonomic predictability among the component communities is demonstrated by the presence of four species in all the samples. The importance of host specificity to predictability is shown by the presence of *Urocleidus adspectus*, the only host-specific parasite of yellow perch, in all the local component communities. *Proteocephalus pearsei*, identified as predictable at the continental scale, was also predictable at the local scale. The remaining two species, *Raphidascaris acus* and *Diplostomum* sp. each use yellow perch as an intermediate host demonstrating the status of this host as both predator and prey.

Additional evidence for pattern and structure in the infracommunities is demonstrated by the significant nestedness in all samples, indicating that communities are initially formed by widespread and common species, and

become more species rich by the sequential addition of increasingly rare species. Nestedness supports the interpretation that there is a core group of species that are predictable. Non-random species associations existed in the infracommunities from the Manitoba samples. By contrast, multispecies associations in the infracommunities from the Wisconsin samples did not depart from random. These observations support the existence of both predictable and stochastic aspects to the parasite communities of yellow perch at both continental and local scales. There was dominance in the predictable groups of parasites that are not host specific. Ecological processes acting across spatial scales are responsible for this predictability.

The most important determinant structuring the parasite communities of yellow perch was the presence of a rich invertebrate fauna capable of transmitting parasites. The importance of diet as a contributor to parasite community structure is emphasized by more abundant parasite infracommunities in hosts from habitats with a richer and more diverse invertebrate fauna that transmits parasites. Hosts with broad diets are predicted to have more parasites than hosts with restricted diets. My data collected from yellow perch from five samples in North America were consistent with this in that hosts in an environment with a greater number of potential invertebrate food items had more parasites. Since yellow perch

have non-specialized feeding habits, a richer invertebrate fauna provides a more varied food source and the potential for a richer and more abundant parasite community. This supports the contention that diet and feeding habits are central in structuring yellow perch parasite communities and, based on my data from North America, factors such as host attributes are secondary and sporadic in their influence. Diet also may explain the association between *B. cuspidatus* with *P. pearsei* since they are both transmitted by copepods. Furthermore, the importance of diet and feeding habits in structuring parasite communities may not be limited to yellow perch, or even fresh water fish, but may be a general phenomenon around which other factors structuring parasite communities exist. For example, a richer and more abundant invertebrate community may be capable of supporting a richer and more diverse fish community. More fish species may be a source of more parasite species that potentially can be shared with other host species, such as yellow perch. In my data, a richer fish community did not provide a richer parasite community; a rich invertebrate community to transmit the parasites was still required to produce the richer and more structured parasite communities.

Biotic factors such as host sex, size and age rarely had an affect on parasite community structure and was inconsistent within a sample between

years, and varied depending the type of parasite considered. Genetically based differences in susceptibility to parasite infection are likely to influence the fish parasite community, but these data are beyond the scope of this thesis.

There was limited support for the core-satellite hypothesis in the parasite communities of yellow perch, despite the taxonomic predictability and nestedness within and among samples. This represents the first time parasites have been used explicitly to test the predictions of the core-satellite hypothesis. At the regional scale, there was no evidence for bimodality of species distribution, but there was a positive correlation between distribution and abundance. At the local scale, the majority of communities had neither a bimodal distribution nor a positive correlation between distribution and abundance. The absence of a positive correlation between distribution and abundance at this scale is intriguing, since it has been suggested that this is a general property of species distribution. Perhaps this is a consequence of the typical negative binomial distribution of parasite species distribution, or that generalities applicable to free-living species do not automatically translate to parasites. In local communities with bimodality of species distribution, the majority of the core species were not host specific and used fish as intermediate hosts to transmit to a piscivorous bird host. In previous studies

in which parasites were used the designation of core species has been manipulated to include host-specific parasites resulting in the general theory that core parasites are host specific. In this study, if core species are present, they are not host-specific, with the exception of *Urocleidus adspectus*. The two parasites that mature in fish belong to the suite of parasites that are predictable in yellow perch at the continental scale There may be a process common at local and continental spatial scales. The remaining core species mature in birds, use a wide variety of fish species as intermediate host, and require the bird host to be present in the system. This supports the theory that the patterns predicted by the core-satellite hypothesis are niche-based rather than stochastic immigration and extinction. Perhaps in hosts with a greater number of host-specific parasites it will be the host-specific species that comprise the core. Subsequent studies investigating hosts with a large number of host specific parasites would provide a valuable counterpoint to yellow perch. It may well be that host specificity is a requirement for the predictions of the core-satellite hypothesis to be met using parasite communities.

The origin of associations between or among taxa is inevitably tied to the origin of the taxa themselves. The origin of the associations between yellow perch and its predictable parasites in North America must account for

how the host and the parasites came to be in the same area and how they came to be together.

Percids, including species in the genus *Perca*, are present in North America and Eurasia. At some point, there had to be dispersal between North America and either Europe and Asia to account for the present distribution. Evaluating the barriers and connections for dispersal between the continents leads to the following conclusions. Based on fossil data, *Perca* was well established in North America prior to Pleistocene glaciation. The hypothesis that *Perca* dispersed across Beringia before or during the Pleistocene is not supported because of the barriers presented by the fast flowing waters of the western cordillera, as well as the mountains themselves. This leaves the North Atlantic route as the route by which *Perca* or its ancestors dispersed between North America and Europe and dates *Perca* to the Eocene (53 mybp - 37 mybp). Therefore it is not unreasonable to propose that *Perca* was present in North America during the Eocene which is older than currently recognized by the fossil record. Which continent is ancestral is unclear based only on the fish species. Parasites might provide some insight into this question. There are more parasite species reported from *P. flavescens* than from *P. fluviatilis*, and the only host specific parasite is in association with *P. flavescens*. This could support the

interpretation that there is a longer association between *Perca* and North America than *Perca* and Europe and that dispersal was from North America to Europe. Interpreting the parasite data in this way assumes that hosts in their area of origin will harbour more parasite species, and that these hosts will have more host specific parasites. The validity of these assumptions is arguable, but it does raise the interesting hypothesis that North America is the origin of the Percidae and they dispersed into Europe across the North Atlantic and then into Asia.

The parasites predictably present with yellow perch in North America all either originated in North America, or have an ancestral Holarctic distribution. In combination, the data on the parasites and the host support the interpretation that all the associated taxa have a North American ancestry; they are in the same place because this is where they originated.

Cospeciation may explain the association between yellow perch and its predictable parasites. However, the data do not support such a hypothesis. The associations of yellow perch with *D. cotylophora*, *B. luciopercae*, *B. sacculata* and *C. cooperi* all are best explained by host switching. In none of these examples is a hypothesis of cospeciation supportable. Even host specific *Urocleidus adspectus* is associated with yellow perch because of host switching. The lineage including *Urocleidus adspectus* is characterized

by ecological diversification involving multiple host switching from an ancestral association with Centrarchidae. The best potential support for cospeciation involves the association between *P. flavescens* and *P. pearsei* in North America and *P. fluviatilis* and *P. percae* in Eurasia. Since both hosts are sister species, if the parasites also are sister species then a hypothesis of cospeciation could be supported. However, the sister species to *P. pearsei* is *P. osculatus*, and these two species are well separated from *P. percae*. As a consequence, cospeciation does not explain the association between yellow perch and *P. pearsei*. There also is no support for cospeciation as an explanation for the association between yellow perch and the other parasites considered. These observations support the hypothesis that the lineage including *U. adspectus* is one of ecological diversification involving host switching into many different taxa from the ancestral association with Centrarchidae. Ecological sympatry of the hosts would explain this host switching. Therefore, the parasite communities of yellow perch are structured by ecological factors and are driven by transmission dynamics through the feeding habits of the host. This may have wider implications for the investigation of parasite communities. If hosts have predictable feeding habits, involving prey that is capable of transmitting parasites, then those food-transmitted parasites should have the same degree

of predictability as the feeding habit. Furthermore, such parasites might reasonably be considered to be a biological trait of the host and provide additional insights into the host biology.

The title of this thesis is "Parasite communities of yellow perch (*Perca flavescens* [Mitchill]): patterns, processes and origins of associations." I have demonstrated that there are repeatable patterns at the continental scale that are shared by both yellow perch in North America and its sister species the Eurasian perch. I also have demonstrated there are repeatable patterns in both local component communities and infracommunities of yellow perch in North America. I propose that one of the processes responsible for these local patterns is host feeding on rich invertebrate fauna that is capable of transmitting parasites. Despite this transmission-based process, and the presence of predictable parasites across scales in the parasite communities of yellow perch, there is no support for the core-satellite hypothesis, a model of community structure based on stochastic transmission. The origin of the associations between the predictable parasites and yellow perch are ecologically based, and are not due to cospeciation between the host and parasite. This provides evidence that communities of parasites that have an ecological basis can nonetheless be predictable across spatial scales.

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APPENDIX 1

A critique of diversity and similarity measures commonly used in parasitology

Diversity is a concept that seems obvious but has proven elusive to define (MacArthur, 1965; McIntosh, 1967; Austin, 1968; Eberhart, 1969; Hurlburt, 1971; Whittaker, 1972). Some argue that measuring diversity serves no useful purpose and as a concept should be eliminated (Hurlburt, 1971; MacArthur, 1965). Nonetheless, measures of diversity have been, and still are, widely used in ecological studies, including parasitological studies. The primary purpose has been to detect patterns of diversity in the community and then attempt to define the processes producing those patterns. Despite the criticisms of diversity and uneven approach in its measurement, there are quantifiable components common to any definition of biological diversity: species richness, species evenness and heterogeneity.

Richness refers to the number of species in a community but is unsuitable as the sole measure of diversity because it is biased by sampling effort and does not reflect the proportional abundance of species in a community. To illustrate; consider two communities each with 10 species and a total of 100 individuals. In Community A each species is represented by 10 individuals, while in Community B species 1 is represented by 91 individuals and each of the remaining 9 species is represented by 1 individual. Clearly Community B is dominated by a single species and

should be recognized as being less diverse than Community A. In this example a simple species count would consider each community to be equally diverse.

Evenness is a measure of how species are represented in a community and is maximized when all species have equal abundance. There are many measures of evenness available, some of which are used to compare values to a theoretical distribution and others which do not. Routledge (1983) argued that an evenness measure should (1) depend only on species proportional abundances and (2) decrease in value either by the addition of rare taxa or by decreasing the abundance of the rarest taxa. Routledge (1983) demonstrated that none of the available measures met these basic requirements. Evenness is dependent on the number of species in the community and as a measure of diversity is subject to the same criticisms as richness.

Heterogeneity describes diversity by combining species richness with evenness and for many ecologists is synonymous with diversity (Hurlburt, 1971; Peet, 1974; Routledge, 1979; Washington, 1984; Krebs, 1989). I concur with this definition of diversity. There is a wide array of indices available to measure and describe heterogeneity. Parasitologists have relied

principally on three heterogeneity indices to measure diversity; Shannon-Wiener index, Brillouin's index and Simpson's index and I will focus on these three.

There is a lack of consensus on how to measure diversity, and the use of indices with unsuitable properties. Therefore, an examination of these indices is warranted. Real data from perch parasite communities collected from two localities in Manitoba and three localities in Wisconsin and simulated data sets were analyzed using the programs DIVERS and SIMILAR (Krebs, 1989). I examined how changes in richness, evenness and sample size affected those diversity indices commonly used in parasitology.

A measure of diversity should reflect changes in species richness and in evenness. The index should not be sensitive to changes in absolute numbers of individuals in the community (what I consider populousness) since this is a reflection of sampling effort. I agree with Whittaker (1972) that diversity is irrevocably tied to species richness, and as such should be interpretable by reference to numbers of species.

Simpson's index D (Simpson, 1949) is a measure of the probability that two individuals randomly selected from the community belong to the same species. There are three versions of this index and two methods of

calculating it. The original formulation is calculated as: $D = \sum (p_i^2)$ where D = Simpson's index and p_i = the proportion of species i in the community. The community decreases as this value approaches 1. The complement of Simpson's (1-D) represents the probability that two randomly chosen individuals are different species and is more commonly calculated since values closer to 1 reflect greater diversity. The reciprocal, (1/D), also is used as a measure of heterogeneity and can range from 1 (1 species in the community) to whatever is the number of species present in the community (maximum diversity).

According to Pielou (1969) the original formula is correct only for an infinite population and has been corrected (Pielou, 1969) for finite populations as:

$$1 - D = 1 - \sum_{i=1}^{s} \left[\frac{n_i(n_i-1)}{N(N-1)} \right]$$

where n_i = number of individuals of species i in the sample, N = total number of individuals in the sample and s = number of species in the

sample. This formulation is unsuitable as it is biased by sample size since it is based on the absolute numbers of individuals.

In the original formulation, this index meets the basic requirements outlined; it does not respond to changes in sample size (Table 24), and it responds to changes in richness and evenness (Figs. 15, 16) and as a consequence is suitable as a diversity measure. As measured by this index, the parasite community from the Lake Winnebago sample is most diverse of the sites sampled (Table 25). All of the variations of Simpson's index have been used to describe the diversity of parasite communities. The reciprocal (1/D) produces the easiest value to interpret since the result can be understood in the context of species number.

The Shannon-Wiener index (H') (Shannon, 1948; Wiener, 1949) is a heterogeneity index derived from information theory and measures the uncertainty regarding the identity of an individual randomly selected from the community. This index is calculated as:

$$\mathbf{H'} = \sum_{i=1}^{s} (\mathbf{p}_i)(\mathbf{log_2 p}_i)$$

where H' = index of species diversity, s = number of species, p_i = proportion of total sample represented by i th species, and any base of logarithm can be used. A community with greater diversity will have greater uncertainty associated with the identity of a randomly chosen individual. Greater uncertainty results in higher values of H', and the interpretation of a more diverse community. This index meets the basic requirements I have outlined above (Table 24). As measured by this index the parasite community from Dauphin is most diverse (Table 25).

Brillouin's index (H) is a heterogeneity index derived from information theory and was first proposed as a measure of diversity in ecology by Margalef (1958). Although rarely used in measuring diversity of free-living organisms, this index is commonly used to describe parasite infracommunities. This index is calculated as:

$$H' = \frac{1}{N} \log \frac{N!}{\Pi n_i!}$$

where H = Brillouin's index, N = number of individuals in the sample, N_i = number of individuals in the ith species for i = 1,..., s, and any base of logarithms may be used. Higher index values reflect greater diversity. This

index is sensitive to richness and evenness (Figs. 15, 16) but responds to changes in number of individuals (Table 24) and as a consequence is unsuitable for use as a measure of diversity.

Information theory indices continue to be used as measures of biological diversity despite criticism (Hurlburt, 1971; Washington, 1974). In the context of ecological diversity Hurlburt (1971, pg. 578) asked what is meant by "...number of bits per individual?". Inasmuch as the criticisms regarding their biological validity (Goodman, 1975; Hurlburt, 1971; Washington, 1984) remain unanswered it is difficult to support the use of either Shannon-Wiener or Brillouin's index. Furthermore both fail to recognize the contribution of species richness, however minimal, to diversity since both calculate a single species community as having zero diversity. Shannon-Wiener is firmly entrenched in the ecological literature and of the two meets the criteria I have set. Simpson's index is suitable if calculated in the original form. It has the added advantage that, if calculated in the form of 1/D, it produces a value which can be interpreted in a biologically meaningful way: the number of equally common species which would produce the same index value.

Peet (1974) recognized two types of heterogeneity indices. Type I indices are most sensitive to changes in the abundance of the rarest species while Type II heterogeneity indices are most sensitive to changes in the most common species (Peet, 1974). Shannon-Weiner is a Type I index while Simpson's is a Type II index and the choice of which to use may be dictated by the emphasis one wishes to place on the common or rare species.

Whittaker (1972) described a second category of diversity which concerns how similar, or dissimilar, is the species composition of different communities taken from a variety of habitats or samples. This type of diversity can be described using similarity indices. A variety of measures of similarity have been used by parasitologists, with two being predominant, the Jaccard index (Jaccard, 1902) and any of a number of percent similarity indices.

According to Wilson and Shmida (1984), a measure of between-habitat diversity should have the following attributes. First, it should be capable of detecting changes in the species composition and abundance of the communities being compared. Second, it should be additive, meaning that if a series of communities are compared along a gradient, then the index value should be the same if calculated from the two ends of the gradient or

by adding the values along the gradient. Third, the measure should be independent of community diversity; if not, then species rich and species poor communities cannot be compared. Finally, a measure of similarity should be independent of sample size.

The Jaccard index (J) is a qualitative measure of species overlap (Jaccard, 1902) and is calculated as:

$$\mathbf{J = c / (a + b - c)}$$

where c = the number of species common to both communities, a = the number of species in community a, and b = the number of species in community b. This is a simple index to calculate that claims to compare the overall similarity between two communities. However, this index has several shortcomings.

Jaccard's index detects changes in species composition but not species abundance and thus does not indicate how similar the two communities being compared really are. For example, compare two communities each with 10 taxa of which 5 are common and equally abundant and 5 taxa are equally rare. If the two communities share only the 5 rare taxa the Jaccard value will be 33.3. The same value will be obtained if the two communities share only the 5 common taxa. Obviously the sharing of the common taxa

results in two more similar communities than the sharing only of rare taxa but the Jaccard index will not reflect this.

Jaccard's index also produces different maximum values if there are different numbers of species in each community. For example, hosts collected from 2 different localities are examined and found to harbour 20 parasite species respectively. If these are all the same species then the maximum Jaccard value will be 1 and if they are all different the Jaccard value will be 0. If hosts from one locality have 20 species and hosts from the other locality have 10 species then the maximum number of species that can be shared is 10 and the maximum Jaccard value is 0.5. Since the number of species recorded increases with sampling effort Jaccard values are sensitive to sample size. It would be best to discard the Jaccard index as a means of estimating overall similarity between parasite communities. The same information can be presented simply by reporting the number of taxa in the two communities and how many they share as a table (e.g. Table 26).

A wide variety of indices have been proposed to measure the quantitative similarity between samples (see Huhta, 1979; Wolda, 1981; Wilson and Shmida, 1984; Magurran, 1988; Krebs, 1989). None of these have been shown to be free of bias but those based on proportional

abundance have been found to be most suitable for comparing similarity between communities (Wolda, 1981; Wilson and Shmida, 1984). However, similarities based on proportions will consider two communities of different absolute size but equal proportional representation by the species to be identical, all else being equal. Since this category of indices represents not only how species are shared, but also their relative abundances, these should be used for comparing similarities between parasite communities. This is consistent with diversity being defined in terms of both richness and relative abundances.

Which of the diversity indices is most appropriate for parasite communities is problematic. It is apparent that the various indices highlight different aspects of the community being studied. For example, perch from the Dauphin Lake sample had the most diverse parasite community as measured by Shannon-Wiener, while the Lake Winnebago sample had the highest diversity as measured by Simpson's index. Comparisons between studies are difficult because different patterns emerge when using Simpson's index and the Shannon-Wiener indices. Simpson's index has ease of calculation as a positive attribute and in the form of 1/D is easily interpreted.

None of the indices seem fully appropriate for comparing communities of parasites collected in hosts from different systems. Jaccard's is unsuitable for direct comparisons between communities. Although the percent similarity indices seem to provide the best estimates of overall similarity, they do not account for differences in prevalence when all else may be equal.

The question is not which index to use, but why use them at all. The underlying differences in species richness or evenness are the basis for differences in diversity. If diversity values are to be reported, then observed values and differences must be discussed in the context of differences in richness, or evenness, or both. Simply reporting diversity values in the absence of these explanations provides little more than a bunch of numbers. Furthermore, the lack of consistency in which index to use and consistent approaches to interpreting the resulting values makes comparisons among studies difficult and discourages the development of concepts and hypotheses in a consistent manner.

Table 24. Effect of changing number of individuals in community on values of Simpson's (1-D), Simpson's (1/D), Shannon-Wiener, and Brillouin's index.

No. taxa	No. individuals	No. taxa x no. individ.	D (finite)	D (original)	Shannon-Wiener	Brillouin
10	1000	10 x 100	0.099	0.1	3.322	3.282
10	500	10 x 50	0.098	0.1	3.322	3.251
10	100	10 x 10	0.091	0.1	3.322	3.069
10	50	10 x 5	0.082	0.1	3.322	2.903
10	1275	9 x 125, 1 x 150	0.1	0.1003	3.320	3.287

Table 25. Infection statistics for parasite infections of yellow perch collected from 5 different localities.

All Parasites	Dauphin Lk. (pooled) (n = 165)	Beaufort Lk. (n = 99)	Lk. Winnebago (n = 95)	Green Bay (n = 107)	Lk. Michigan (n = 38)
# infected hosts	157	97	60	99	38
Total # parasite species	18	15	14	10	10
Mean species richness	3.7 ± 2.3	2 ± 1.4	1 ± 1.5	2.5 ± 1.1	3.4 ± 1.2
Simpson's reciprocal (1/D)	4.02	3.94	4.55	3.75	2.94
Shannon-Wiener (H)	2.72	2.42	2.67	2.15	1.88

Table 26. Percent similarity and number of shared species for parasites recovered from yellow perch, *Perca flavescens*, collected from five different waterbodies. Percent similarities are indicated above the diagonal and number of shared species are indicated below the diagonal.

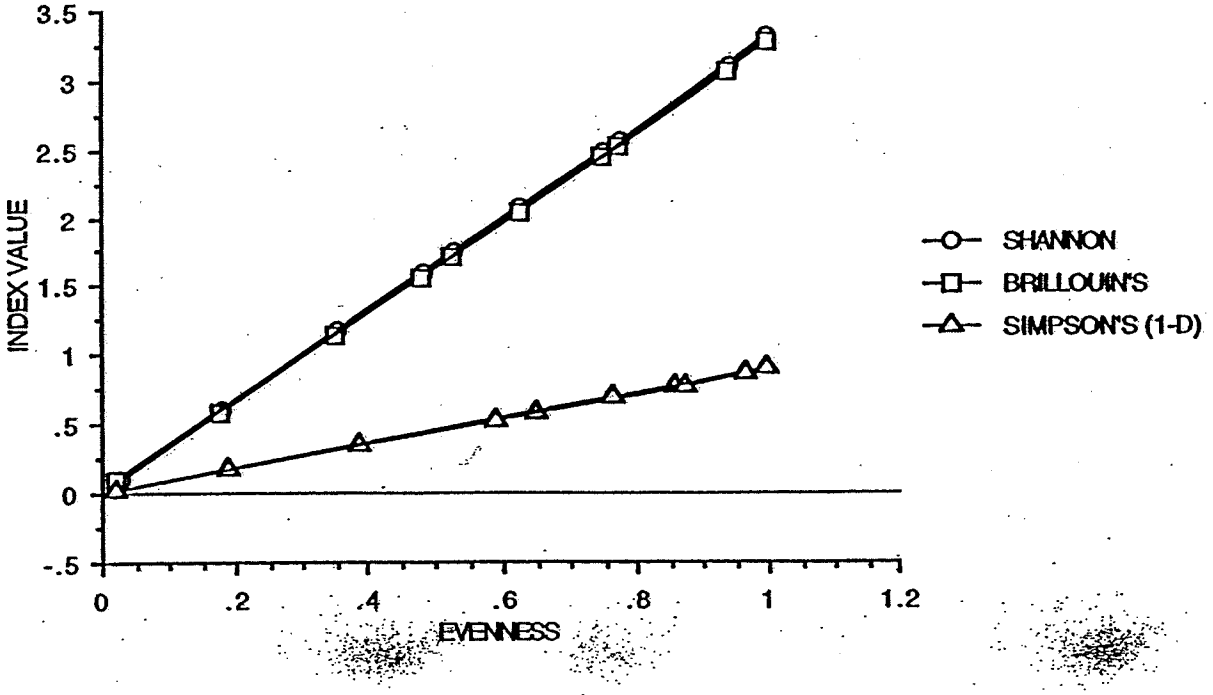
	Dauphin Lk. (18)†	Beaufort Lk. (15)	Lk. Winnebago (14)	Green Bay (10)	Lk. Michigan (10)
Dauphin Lk. (18)†	•	0.514‡	0.278	0.288	0.292
Beaufort Lk. (15)	12*	•	0.443	0.088	0.09
Lk. Winnebago (14)	9	8	•	0.215	0.431
Green Bay (10)	5	6	6	•	0.314
Lk. Michigan (10)	7	7	6	6	•

†Number of parasite species collected from all perch in the indicated water body.

* Number of shared parasite species collected from perch collected from each water body.

‡ Renkonen percent similarity index calculated as: $P = \sum \text{minimum } (p_{1i}, p_{2i})$ where P = percent similarity, p_{1i} = percent of species i in community 1, p_{2i} = percent of species i in community 2.

Figure 15. Values for Brillouin's, Shannon-Wiener, and Simpson's (1-D) indices with changes in evenness. Number of taxa is constant at 10, total individuals is constant at 1000. Δ denotes Simpson's (1/D); o denotes Shannon-Wiener, □ denotes Brillouin's.


INDEX VALUE
3.5
3
2.5
2
1.5
1
.5
0
-.5
0
.2
.4
.6
.8
1
1.2
EVENNESS
SHANNON
BRILLOUIN'S
SIMPSON'S (1-D)

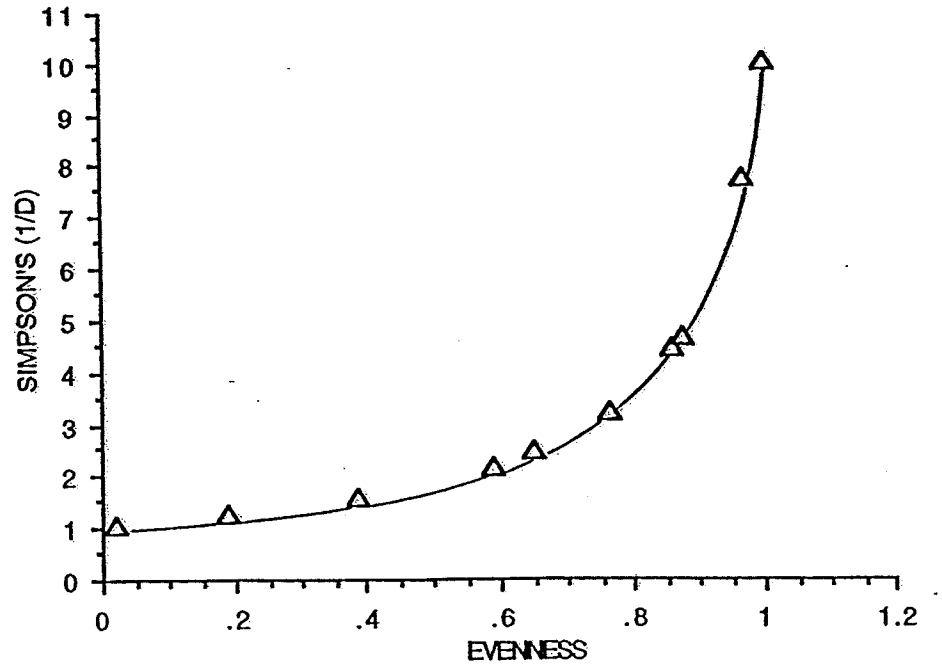
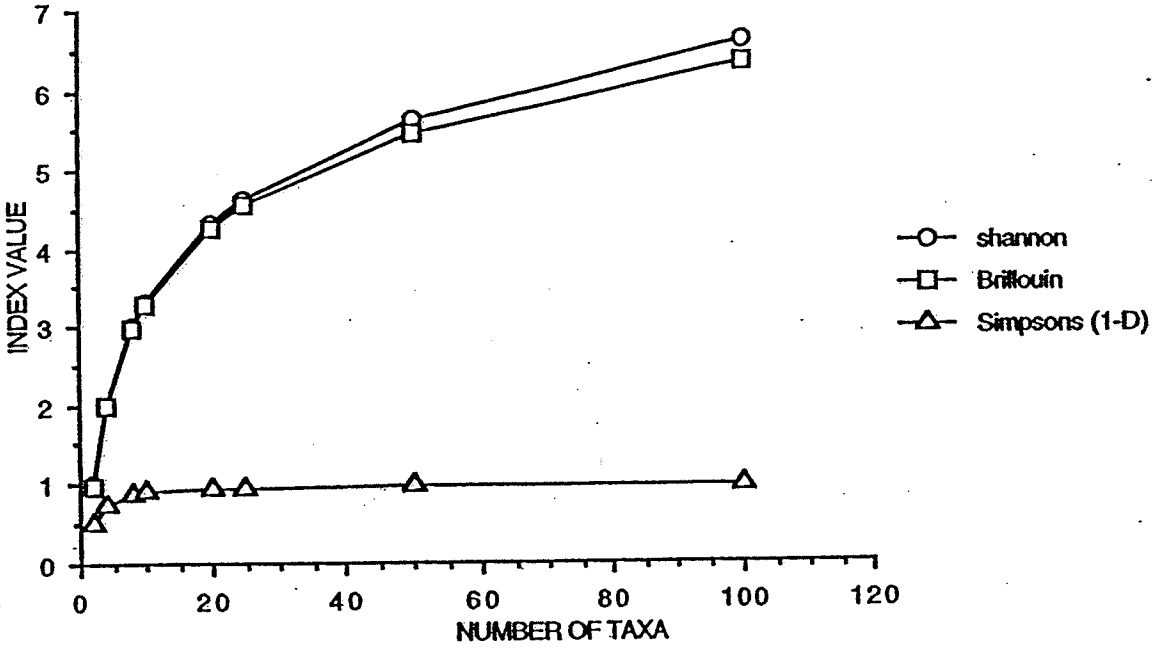
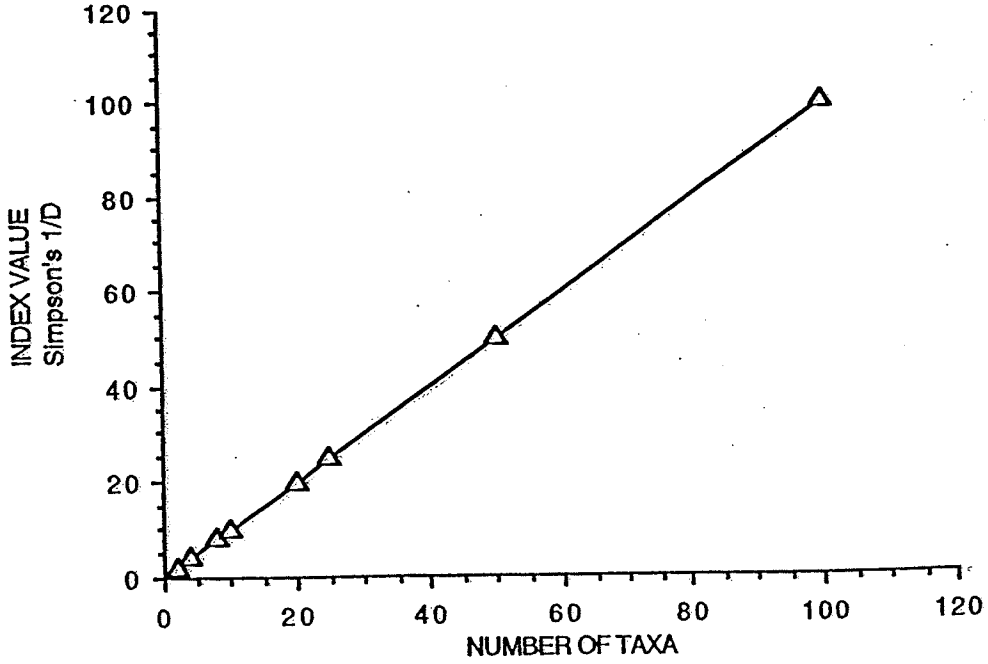

SIMPSON'S (1/D)
11
10
9
8
7
6
5
4
3
2
1
0
0
.2
.4
.6
.8
1
1.2
EVENNESS

Figure 16. Values for Brillouin's, Shannon-Wiener, and Simpson's (1-D) indices with changes in species richness. Evenness is constant at 1, total individuals is constant at 1000.Δ denotes Simpson's (1/D); o denotes Shannon-Wiener, □ denotes Brillouin's.


INDEX VALUE
0
1
2
3
4
5
6
7
0
20
40
60
80
100
120
NUMBER OF TAXA
shannon
Brillouin
Simpsons (1-D)


INDEX VALUE
Simpson's 1/D
0
20
40
60
80
100
120
NUMBER OF TAXA

APPENDIX 2

Cladistic analysis of Nearctic and South American species in the genus *Dichelyne* with a preliminary examination of the phylogeny of Cucullanidae

ABSTRACT: This study on relationships within the nematode family Cucullanidae and new world species in the genus *Dichelyne* is conducted in order to understand the association between *D. cotylophora* (Ward and Magath) and its fish host, the yellow perch (*Perca flavescens* [Mitchill]), in North America. Because recognition of the genus *Dichelyne* has been variable, eight nominal genera in the nematode family Cucullanidae were examined for a preliminary phylogenetic analysis to determine the validity of characters considered to be important in recognizing genera within the family, to test a previous hypothesis of phylogeny and to assess the monophyly of the genus *Dichelyne*. Characters analyzed were based on adult morphology. Results supported a diagnosis of 8 valid genera. The preanal sucker, often considered an important generic character, was homoplasious and, combined with an uncertain optimization for intestinal caecum position, forms the basis for much of the previous lack of agreement in the number of genera and their defining traits. A previous hypothesis of phylogenetic relationships based on a reduction to three genera is not supported. The monophyly of *Dichelyne*, as distinct from *Neocucullanellus* and *Cucullanellus*, was demonstrated by the presence of a dorsal intestinal caecum. A subsequent phylogenetic analysis was

performed on 10 species of the nematode genus *Dichelyne* to test whether coevolution could explain the predictable association between *D. cotylophora* and its host, *P. flavescens*. Characters were based on adult morphology. A single most parsimonious tree supports the interpretation that those species found in hosts from South America and the Pacific are basal to a monophyletic clade found in North America, and that in the North American species, there has been more than one instance of dispersal into marine hosts from freshwater hosts. These results provided no support for cospeciation for the predictable association between *P. flavescens* and *D. cotylophora* in North America.

INTRODUCTION

The nematode, *Dichelyne cotylophora* (Ward and Magath) has been reported from a variety of fish hosts but based on frequency of occurrence, shows a preference for yellow perch (*Perca flavescens* [Mitchill]) as definitive host (Baker, 1984). In Chapter 1, I identified *D. cotylophora* as a member of a suite of parasites predictably associated with yellow perch and also identified a taxonomically different, but ecologically similar suite of parasites predictably associated with the perch (*P. fluviatilis* L.) in Eurasia (Carney and Dick, 1999). Predictable host parasite associations have been explained to be a consequence of either host specificity or coevolution (Brooks and McLennan, 1991, 1993; Choudhury and Dick, 1993, 1998). The predictable suite of parasites in each of the perch species is ecologically based and is the result of the fish hosts having an overall similar biology, particularly in relation to feeding behaviour (Carney and Dick, 1999, 2000). Feeding habits and a diverse invertebrate community are responsible for rich parasite communities of yellow perch in North America and these are the sources of observed predictability within the communities (Chapter 2). However, cospeciation has not been eliminated as an explanation for the predictable association

between yellow perch and and their predictable suite of parasites, in particular *D. cotylophora*, especially since I speculated in Chapter 1 that the absence of *D. cotylophora* in the Hudson Bay drainage system had a historical basis. Cladistic analysis of the genus *Dichelyne* would assist in determining the evolutionary basis for the association between *D. cotylophora* and yellow perch.

The nematode family Cucullanidae Cobbold, 1864 is cosmopolitan in distribution and contains several genera parasitizing marine and freshwater fishes in many families (Petter, 1974). However, consensus has been lacking in the defining characteristics of *Dichelyne*, its constituents, and whether it is a valid genus within the family. For example, *Dichelyne* has been recognized, suppressed, and had other genera placed within it. Lack of consensus on the defining characters has resulted in disagreement on the number of genera within Cucullanidae. Tornquist (1931) recognized 4 genera in the family, *Cucullanus*, *Dacnitis*, *Cucullanellus*, and *Dichelyne*. Characteristics Tornquist (1931) considered important for generic differentiation included the presence and position of an intestinal caecum, and the inclination of the mouth relative to the longitudinal body axis. Tornquist (1931) did not recognize

Neocucullanellus, considering it to be insufficiently defined. Chitwood and Wehr (1934) considered the number of male caudal papillae an important generic character and recognized *Neocucullanellus* as well as the 4 genera defined by Tornquist (1931). By contrast, Campana-Rouget (1957) suppressed *Dichelyne*, *Cucullanellus* and *Neocucullanellus*, and recognized just three genera in the family, *Dacnitis*, *Cucullanus* and *Neocucullanus*, using the inclination of the mouth and the number of preanal papillae as important generic characters.

Yamaguti (1961) recognized two subfamilies, the Cucullaninae and Dacnitoidinae using the presence or absence of an intestinal caecum and the number of ovaries as defining traits. Within Cucullaninae, Yamaguti (1961) recognized *Neocucullanus*, *Cucullanus*, and *Indocucullanus*. Generic traits included a pointed tail, a dorsal curve of the body at the anterior end, a preanal "sucker" and buccal capsule armature. Within Dacnitoidinae Yamaguti (1961) considered *Dacnitoides*, *Cucullanellus*, *Dichelyne*, and *Neocucullanellus* to be valid genera using a terminal horn on the tail, a preanal "sucker", the presence and position of an intestinal caecum, caudal alae, and the number of ovaries as diagnostic characters.

Maggenti, (1971) in a review of Cucullanidae used the presence of a male preanal "sucker" to distinguish *Neocucullanus*, *Dacnitoides*, *Cucullanellus*, *Cucullanus* and *Bulbodacnitis* from *Indocucullanus*, *Dichelyne* and *Neocucullanellus*. Maggenti (1971) considered the presence and position of an intestinal caecum, the number of caudal papillae and the orientation of the mouth relative to the body axis also to be generically important traits.

Petter (1974) reduced the number of genera in the Cucullanidae to *Cucullanus*, *Truttaedacnitis* and *Dichelyne* and proposed a phylogenetic hypothesis for these genera. The characters used to define the genera and develop the hypothesis of relationships included the intestinal caecum, male adult size, cuticle thickness and relative position of the caudal papillae.

A resolution of the number of genera in Cucullanidae is important in order to test if cospeciation or ecological factors better explain the predictable association between yellow perch and *D. cotylophora*. However, a preliminary phylogenetic analysis of the family is required to determine the number of genera and their characteristics, and whether *Dichelyne* is a valid genus. A cladistic analysis can be used to develop

hypotheses of relationships among taxa and be used to assess *a posteriori* the status of different characters as defining traits. Thus, the apomorphic morphological characters for genera, the number of genera in the family, can be determined. If a cospeciation between *P. flavescens* and *D. cotylophora* can be established, then the extant association can be considered to have a historical evolutionary basis. By contrast, if a cospeciation explanation cannot be shown, then other explanations are needed. The primary objective of this chapter is to determine whether there is a cospeciation origin for the association between *Perca flavescens* and *D. cotylophora*. Since this requires demonstrating the monophyly of the genus *Dichelyne*, a second objective is to evaluate genera in the family Cucullanidae, define characters and assess the hypothesis of phylogeny for the group (Figure 17) as proposed by Petter (1974).

MATERIALS AND METHODS

Phylogenetic analysis of 8 nominal genera in the family Cucullanidae was performed using 7 presumed homologous characters derived from adult morphology (Table 27). Character data were obtained by reference to the literature and examination of museum specimens obtained from the U.S. National Parasite Collection, Beltsville, Maryland (USNPC) and the University of California Davis nematode collection (UCDNC). Cladistic analysis was performed using the computer program PAUP 3.1 (Swofford, 1993). Character polarity was determined using the outgroup comparison method (Watrous and Wheeler, 1981; Maddison et al., 1984) using species from the family Seuratidae as outgroups. The PAUP options mulpars, branch and bound, and global branch swapping were invoked to ensure the most parsimonious trees were identified. Farris optimization (Farris, 1970) was employed to examine the fit of each character transformation. The following characters and their states were analyzed to develop a hypothesis for the phylogeny of genera in the family Cucullanidae.

Cucullanidae

1. Preanal "sucker". In some genera there are species with males having a preanal "sucker" while other genera do not. The absence of this structure is considered to be plesiomorphic and the presence to be apomorphic.

2. Mouth inclination. Some species have a mouth that is dorsally inclined relative to the longitudinal body axis and others have a mouth that terminates perpendicular to the body axis. A dorsally inclined mouth is considered apomorphic and the perpendicular mouth plesiomorphic.

3. Presence or absence of an intestinal caecum. The presence of an intestinal caecum varies among genera. The absence is considered to be plesiomorphic and the presence to be apomorphic.

4. Caecum position. If a caecum is present, it is either dorsal or ventral in orientation. The outgroup lacks a caecum and this is considered plesiomorphic. There is no *a priori* reason to consider either ventral or dorsal positioning to be apomorphic relative to the other and, accordingly, this character is analyzed using the unordered option in PAUP.

5. Number of caudal papillae on the male. The majority of species within genera of the Cucullanidae have 11 caudal papillae. Species in

Neocucullanus and *Neocucullanellus* have more than 11 papillae. Having 11 papillae is considered to be plesiomorphic and more than 11 papillae to be apomorphic.

6. Number of ovaries. Some genera have a single ovary while others have two. The single ovary is considered to be plesiomorphic and having two ovaries is considered apomorphic.

7. Oesophastome. The head arises from two sources, from an anterior region of primary embryonic invagination called the oesophastome, or from an anterior region of secondary overgrowth termed the cheilostome (Inglis, 1967). The presence of an oesophastome is found only in species of the Cucullanidae and constitutes a synapomorphy defining the monophyly of genera within the family.

Dichelyne

Cladistic analysis of 10 species of *Dichelyne* was performed using 8 homologous characters derived from adult morphology (Table 28). Character data were obtained by examining type and voucher specimens obtained from the U.S. National Parasite Collection, Beltsville, Maryland (USNPC) and the University of California Davis nematode collection (UCDNC), specimens from yellow perch samples from Green Bay,

Wisconsin (JPC) and supplemented by referral to primary literature. Cladistic analysis was performed using the computer program PAUP 3.1 (Swofford, 1991) following the same procedures as for the analysis of genera within the Cucullanidae using species of *Cucullanus* and *Bulbodacnitis* as outgroups.

Specimens examined

Dichelyne bullocki Stromberg and Crites USNPC no. 71995 (2 specimens); *Dichelyne cotylophora* USNPC nos. 58272, 52093, 52094, 78867, 48397, 86804 (27 specimens); *Dichelyne diplocaecum* Chandler USNPC no. 39544 (1 specimen); *Dichelyne fastigatus* Chandler USNPC no. 39543 (1 specimen); *Dichelyne laticeps* Baylis no. USNPC 81827 (5 specimens); *Dichelyne lepisosteus* Casto and McDaniel USNPC nos. 61491, 61492 (2 specimens); *Dichelyne robusta* (Van Cleave and Mueller) USNPC nos. 76500, 80743 (2 specimens); *Cucullanus pulcherrinus* Barreto USNPC no. 31737 (1 specimen); *Cucullanus lutjani* Schmidt and Kuntz USNPC no. 71388 (2 specimens); *Cucullanus okinawanus* Hasegawa, Williams, Jr. and Bunkley-Williams USNPC no. 81826 (2 specimens); *Bulbodacnitis ampullastoma* Maggenti UCDNC nos. 3391, 3393, 3398, 3396, 3407, 3408, 3411, 3412 (9 specimens).

Vouchers from Green Bay have been submitted for accession number to the USNPC.

Character argumentation

The following characters and their states were analyzed to develop a hypothesis of phylogeny of the species in the genus *Dichelyne*.

1. Presence of a preanal "sucker". Two states are recognized. The absence of a preanal "sucker" on males is considered to be plesiomorphic based on the previous analysis of the genera. The presence of a preanal "sucker" is considered to be apomorphic.

2. Tail terminated with a single spine. Some species of *Dichelyne* have a spine on the tip of the tail while others do not. The plesiomorphic condition is considered to be an aspinose tail while the presence of a spine is considered to be apomorphic.

3. Relative size of the spicules. Some species of *Dichelyne* have large spicules while others have comparatively smaller spicules. Two states are recognized. The plesiomorphic state is spicules less than or equal to 20% total body length. The apomorphic state is spicules larger, measuring greater than 20% of total body length.

4. Presence of a dorsal anteriorly directed caecum. The presence of an intestinal caecum is important in identifying genera within the family Cucullanidae. *Dichelyne* is recognized here as being monophyletic by the presence of a dorsal intestinal caecum. This is synapomorphic for the genus and defines the group as monophyletic.

5. Excretory pore position. Some species of Dichelyne have the excretory pore anterior to the junction of the oesophastome and the intestine while others have the pore posterior to this junction. The posterior position is considered apomorphic while the anterior position is considered plesiomorphic.

6. Dereid position. The dereids are located either posterior or anterior of the oesophagous/intestine junction. Outgroup comparison did not polarize this character so it is analyzed using the unordered option in PAUP

7. Pattern of male caudal papillae. There are two basic patterns observed for the male caudal papillae. One has 5 pairs of papillae plus a pair of phasmids posterior to the anus, whereas the other has 3 pairs of papillae plus a pair of phasmids posterior to the anus and 2 pairs of papillae adanal. It was not possible to polarize this character using outgroup comparison so it is analyzed using the unordered option in PAUP.

8. Teeth. The teeth surrounding the oral opening in species of *Dichelyne* come in two forms. One is a narrow blade-like form and the other is a shark-tooth shape, with a broad "root" curving and tapering to a point. The plesiomorphic state is a narrow blade-like form and the apomorphic shape is the shark-tooth form.

Species incertae sedis

Dichelyne diplocaecum Chandler was described based on two female specimens from a single *Ictalurus furcatus* (Lesueur) from Galveston Bay, Texas. This species has both dorsal and ventral intestinal caecae which was used to justify reducing *Cucullanellus* to a subgenus of *Dichelyne*. However, my phylogenetic analysis of the genera in the family Cucullanidae has shown that the presence of a ventral caecum is a valid synapomorphy for *Cucullanellus* and *Neocucullanellus* and dorsal caecum is a synapomorphy for *Dichelyne*. If *D. diplocaecum* is in fact a valid species, then the presence of 2 caeca represents a synapomorphy for a monotypic genus. However, in the absence of more material validating this species, I consider it to be *incertae sedis* and have not included it in this analysis.

RESULTS

Phylogenetic analysis of the genera in the family Cucullanidae produced 3 trees of 11 steps (Figure 18) with a consistency index of 0.818 (Table 29). Incongruence of these trees is related to the optimization of characters 1 (preanal sucker) and 4 (position of caecum), producing uncertainty regarding the relationships among *Dichelyne*, *Cucullanellus* and *Neocucullanellus*, and in the placement of *Neocucullanus* (Figure 19). Common elements include a monophyletic clade, comprising *Dichelyne*, *Neocucullanellus* and *Cucullanellus*, and a monophyletic clade, containing *Cucullanus*, *Truttaedacnitis* and *Bulbodacnitis*. Which of these clades is relatively more basal is undetermined from this analysis.

The presence of a caecum is synapomorphic for the grouping of *Dichelyne Neocucullanellus* and *Cucullanellus*, and within this clade, *Dichelyne* is recognized as monophyletic by virtue of the anteriorly directed dorsal caecum while *Neocucullanellus* and *Cucullanellus* have a ventral caecum. Whether a ventral or dorsal caecum is plesiomorphic is unclear.

Cladistic analysis of the *Dichelyne* data matrix (Table 28) produced a single most parsimonious tree of 15 steps (Figure 20), with a consistency index of 0.733 (Table 29). The relationship between *D. leporini*, found in South American freshwater fishes, and *D. laticeps*, recorded from marine fishes in Japan, is unresolved. This hypothesis of phylogeny supports the interpretation that species present in North America form a monophyletic group that is apomorphic to those species reported from South America and the Pacific. Ancestral habitat type unambiguously optimizes to freshwater with three independent dispersals into hosts found in a marine environment (Figure 21).

DISCUSSION

The presence of an oesophastome is a synapomorphy for the family and identifies the Cucullanidae as a monophyletic group.There has been little consensus regarding the number of genera in the family Cucullanidae due to disagreements regarding the generic importance of different morphological characters such as the presence and position of a caecum and presence of a male preanal "sucker". My analysis found these characters to be incongruent with each other and also to be homoplasious, but a dorsal caecum is a diagnostic character defining *Dichelyne* (Figure 18). Furthermore, the presence of a preanal "sucker" in the male has arisen twice but does not constitute a synapomorphy for any single genus. This trait also is one of the two characters which is the source of ambiguity in the three most parsimonious trees (Figure 18). The trees represented in Figure 19-A and 8-B support the interpretation that the preanal sucker constitutes a synapomorphy defining the clade containing *Neocucullanus*, *Bulbodacnitis*, *Truttaedacnitis* and *Cucullanus* and also as an independent apomorphy for *Cucullanellus*. These hypotheses (Figures 8-A, 8-B) would be consistent with convergent evolution of the preanal sucker in those groups having this trait. The tree

represented in Figure 19-C supports the interpretation that the preanal sucker is a synapomorphy separating all the other species in the genus from *Indocucullanus* and has been lost (reversal) in *Neocucullanellus* and some species of *Dichelyne*. Heterochrony, resulting from paedomorphic development (Alberch et al., 1979), can result in trait reversals and may explain the loss of this trait. It is not possible to choose between these different tree topologies or the potential evolutionary mechanisms explaining the appearance of this trait using the available data. Nonetheless, the presence or absence of a preanal sucker does not unambiguously characterize any single genus unless optimization of this character represented by Figure 19-A and 8-B is correct, in which case it represents a synapomorphy defining *Cucullanellus*.

The other character causing disagreement among the different trees is whether the ventral or dorsal caecum is plesiomorphic. If the dorsal state is plesiomorphic (Fig. 8-A) then *Dichelyne* is the sister taxon to *Cucullanellus* and *Neocucullanellus*. If the ventral position is plesiomorphic (Figure 19-B, 8-C), then the dorsal state is apomorphic for *Dichelyne*. The evolution of this trait is ambiguous since there is no reason to choose between these interpretations.

The generic synonymies and evolutionary hypothesis for genera in the family Cucullanidae (Figure 17) proposed by Petter (1974) are not supported by my analysis. Petter (1974) proposed a new classification for Cucullanidae using a restricted set of morphological characters and the correlation between these characters and the phylogenetic position of their hosts. Petter (1974) synonymized three genera into *Truttaedacnitis* (*Dacnitis* sensu Tornquist, 1931; *Bulbodacnitis* sensu Maggenti, 1971) and considered these to be basal species associated with the most primitive fishes (Figure 17). The other two genera that Petter (1974) recognized were *Cucullanus* occurring in Teleostei including Salmoniformes and *Dichelyne* with subgenera *Cucullanellus*, *Dichelyne*, and *Neocucullanellus* occurring only in the most advanced teleosts. Characters used by Petter (1974), but not found to be useful for cladistic analysis in this study, included the length:width ratios, thickness of the cuticle, position of caudal papilla 9 and host type. As a consequence the phylogeny proposed by Petter (1974) was based on 2 morphological characters and an assumed coevolution with primitive hosts having primitive parasites. Nevertheless, the analysis by Petter (1974) has been

influential in formulating opinion on the relationships within this family (Gupta and Masoodi, 1982).

My recognition of the valid genera in Cucullanidae is consistent with the cladistic analysis by Choudhury and Dick (1996) who demonstrated the validity of *Truttaedacnitis*, contrary to other studies (e.g. Moravec, 1994). Furthermore, I have identified potential synapomorphies for all genera included in my analysis, with the exception of *Cucullanus*. Although the clades containing *Cucullanus*, *Truttaedacnitis* + *Bulbodacnitis*, and *Dichelyne* + *Cucullanellus* + *Neocucullanellus* each are monophyletic, which is consistent with Petter (1974), none of the trees support an interpretation that the *Truttaedacnitis* clade is basal relative to the other genera (Figure 18). Petter (1974) did not explicitly polarize the characters independent of the host taxa, resulting in the conclusion that *Truttaedacnitis* is basal because species are associated with "primitive" fishes and *Dichelyne* derived because species are associated with "advanced" fishes. My analysis, developed independent of host systematics, does not support this argument, since *Truttaedacnitis* is not basal on any of the trees reported here, and *Dichelyne* is no more derived than *Cucullanus* or *Truttaedacnitis*.

Dichelyne as a valid genus, based on the presence of a dorsal caecum, and by the phylogenetic hypothesis presented here it appears that *Dichelyne* spp. in South America and in the Pacific are ancestral relative to those in North American waters. Furthermore, this hypothesis supports the interpretation that those species present in North America constitute a monophyletic lineage resulting from a single dispersal into North America, followed by speciation.

While *Dichelyne* spp. are reported from both freshwater and marine hosts, this analysis supports the interpretation that the ancestral habitat was in freshwater. My analysis supports two independent instances of diversification into a marine host from freshwater in North America; *D. cylindricus* and *D. fastigatus* (Fig. 10). Anderson (1984, 1988) has suggested that zooparasitic nematodes were first terrestrial and subsequently acquired aquatic hosts. If this is correct, then the ability to acquire hosts in either a marine or freshwater environment may not be evolutionarily unconstrained, but depend more on ecological considerations such as host sympatry. This would be consistent with my contention that the *Dichelyne* association with perch is ecologically based, especially since the *Dichelyne* spp. recorded from marine

environments in North America were actually from more brackish-water habitats at the heads of bays. Interestingly, there is no evidence for cospeciation between species of *Dichelyne* and their respective fish hosts. This is reinforced by the independent acquisition of marine fishes as hosts by *D. cylindricus* and *D. fastigatus* and by the observation that *D. cotylophora* in yellow perch is the sister taxon to *D. lepisosteus* and *D. bullocki*. *Dichelyne lepisosteus* has only been reported from gars, a group of fishes evolutionarily much older than perch (Carroll, 1988). This absence of cospeciation seems to be a general phenomenon of *Dichelyne*, a trait *D. cotylophora* has inherited.

This analysis does not support a hypothesis of cospeciation to explain the predictable association between yellow perch and *D. cotylophora* reported in previous chapters (Carney and Dick, 1999, 2000). The association between *D. cotylophora* and yellow perch in North America is best explained as a consequence of a host switch from a pre-existing association with another freshwater host. This appears to be a general pattern for species in this genus since there is no evidence for cospeciation between *Dichelyne* and their respective hosts. Acquiring parasites as a consequence of a host switch or host capture seems best

explained by having similar ecological requirements with a sympatric host from which the new parasite is acquired.

Table 27. Character matrix for numerical phylogenetic analysis of 8 genera in the nematode family Cucullanidae.

	Characters						
Species	1	2	3	4	5	6	7
Outgroup	0	0	0	0	0	0	0
Cucullanus	1	1	0	0	0	2	1
Truttaedacnitis	1	1	0	0	0	2	1
Dichelyne	0	0	1	1	0	2	1
Cucullanellus	1	0	1	2	0	2	1
Indocucullanus	0	0	0	0	0	2	1
Neocucullanus	1	0	0	0	1	2	1
Bulbodacnitis	1	1	0	0	0	1	1
Neocucullanellus	0	0	1	2	1	2	1

*Outgroup is a composite, based on outgroup comparisons of several taxa, used to facilitate computer analysis.

Table 28. Character matrix for numerical phylogenetic analysis of 10 species of *Dichelyne*.

	Characters							
Species	1	2	3	4	5	6	7	8
Outgroup*	0	0	0	0	0	0	0	0
D. bullocki	0	1	1	1	1	1	1	0
D. cotylophora	0	1	0	1	1	1	1	0
D. cylindricus	1	?	?	1	1	2	?	1
D. elongatus	0	1	0	1	0	0	1	0
D. fastigatus	1	1	0	1	1	1	1	0
D. moraveci	1	0	1	1	0	0	2	0
D. laticeps	0	0	0	1	0	0	2	0
D. leporini	0	0	0	1	0	0	2	?
D. lepisosteus	0	0	1	1	1	1	1	2
D. robusta	1	0	0	1	1	1	2	1

*Outgroup is a composite, based on outgroup comparisons of several taxa, used to facilitate computer analysis.

Table 29. Diagnostic statistics for phylogenetic trees resulting from PAUP analysis of the matrices for Cucullanidae and *Dichelyne*.

Statistic	Cucullanidae	*Dichelyne*
Number of characters	7	8
Number of steps	11	15
Consistency index (CI)	0.818	0.733
CI (corr)*	0.75	0.714
Retention Index (RI)	0.778	0.810
Rescaled consistency index (RC)	0.636	0.594

*Consistency index with uninformative characters removed.

Figure 17. Reconstruction of the phylogenetic hypothesis proposed by Petter (1974).

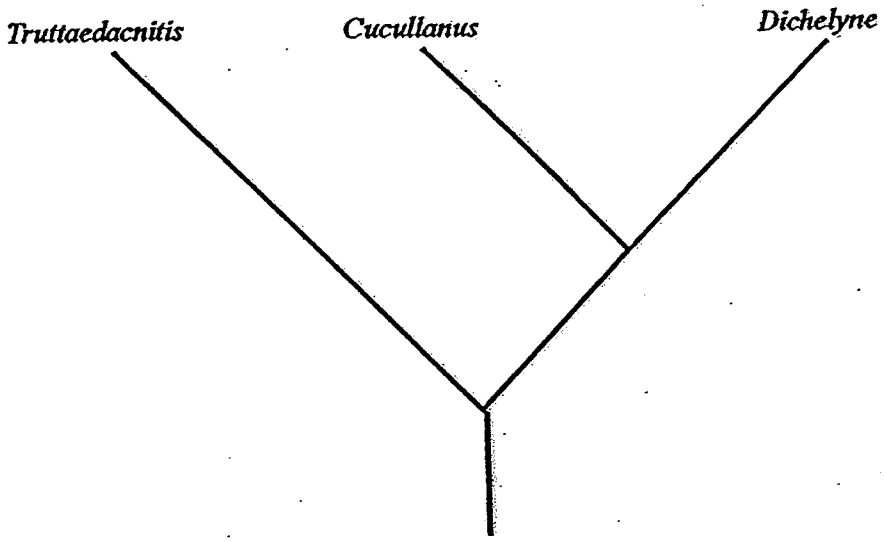
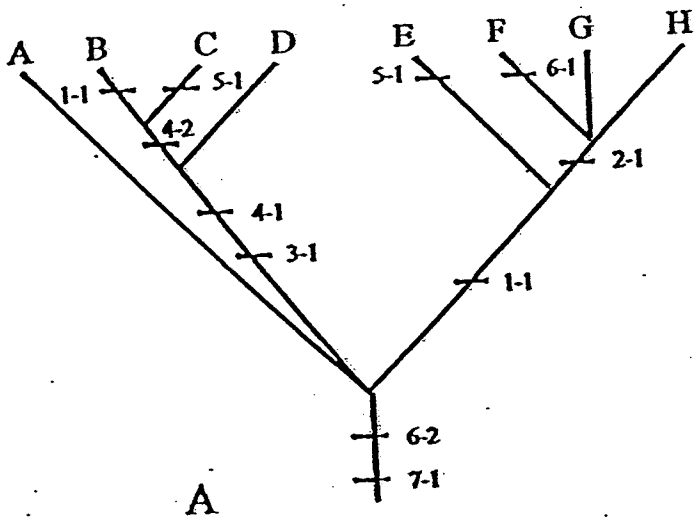
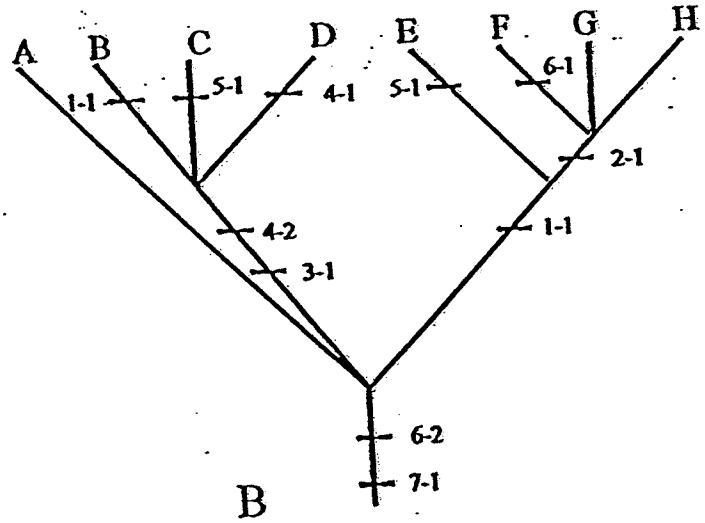

Truttaedacnitis
Cucullanus
Dichelyne

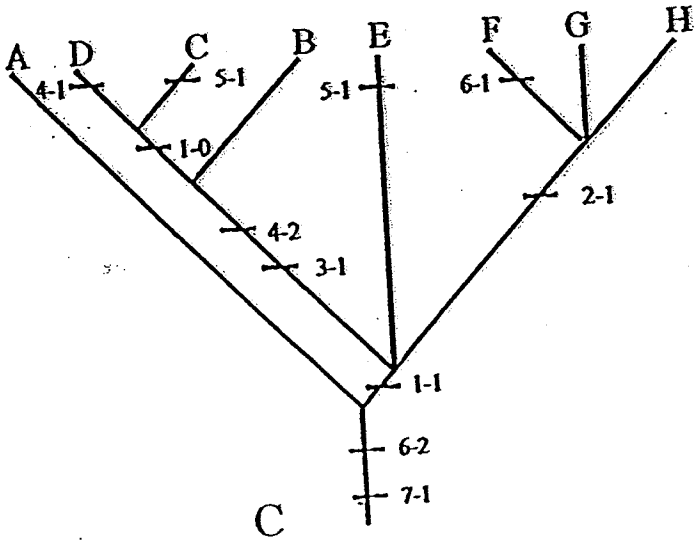
Figure 18. Three most parsimonious trees for genera in the family Cucullanidae generated by analysis of the data matrix shown in Table 27. Letters refer to the following genera: A, *Indocucullanus*; B, *Cucullanellus*; C, *Neocucullanellus*; D, *Dichelyne*; E, *Neocucullanus*; F, *Bulbodacnitis*; G, *Truttaedacnitis*; H, *Cucullanus*. Refer to text for character identification.


A
B
C
D
E
F
G
H
1-1
5-1
4-2
4-1
3-1
5-1
6-1
2-1
1-1
6-2
7-1

A

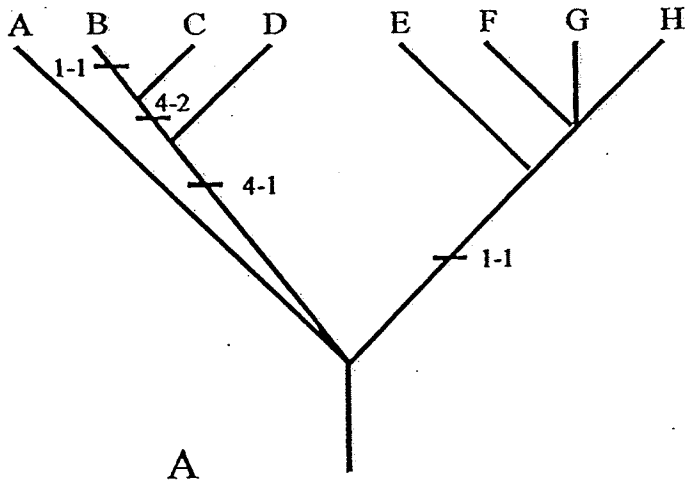

A
B
C
D
E
F
G
H
1-1
5-1
4-1
5-1
6-1
2-1
4-2
3-1
1-1
6-2
7-1

B

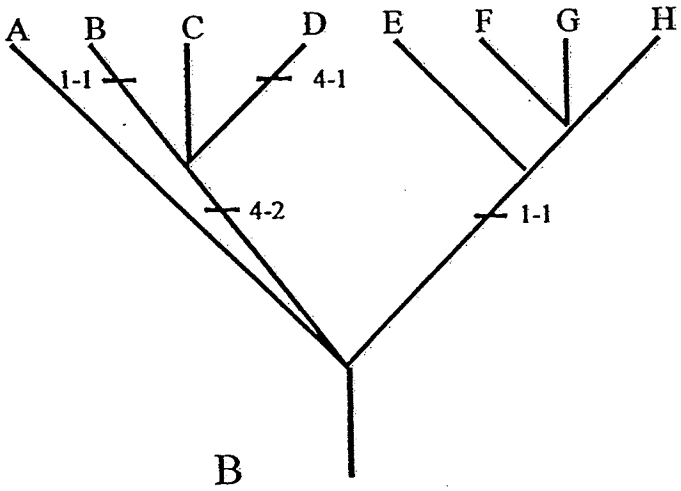

A
D
C
B
E
F
G
H
4-1
5-1
5-1
6-1
1-0
2-1
4-2
3-1
1-1
6-2
7-1

C

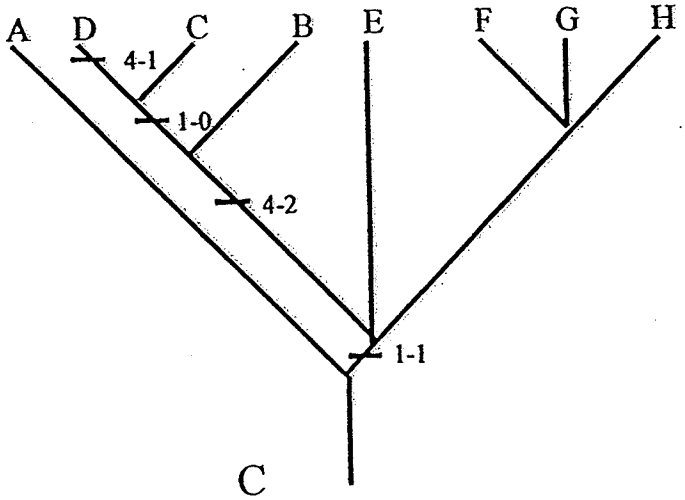
Figure 19. Comparison of optimization of characters 1 and 4 on the trees shown in Figure 22. Letters refer to the following genera: A, *Indocucullanus*; B, *Cucullanellus*; C, *Neocucullanellus*; D, *Dichelyne*; E, *Neocucullanus*; F, *Bulbodacnitis*; G, *Truttaedacnitis*; H, *Cucullanus*.



A



B



C

Figure 20. Most parsimonious phylogenetic tree generated by phylogenetic analysis of the data matrix shown in Table 28 for 11 species in the genus *Dichelyne*. Letters refer to the following species: A, *D. elongatus*; B, *D. leporini*; C, *D. laticeps*; D, *D. moraveci*; E, *D. fastigatus*; F, *D. robusta*; G, *D. cylindricus*; H, *D. cotylophora*; I, *D. lepisosteus*; J, *D. bullocki*. Refer to text for character identification.

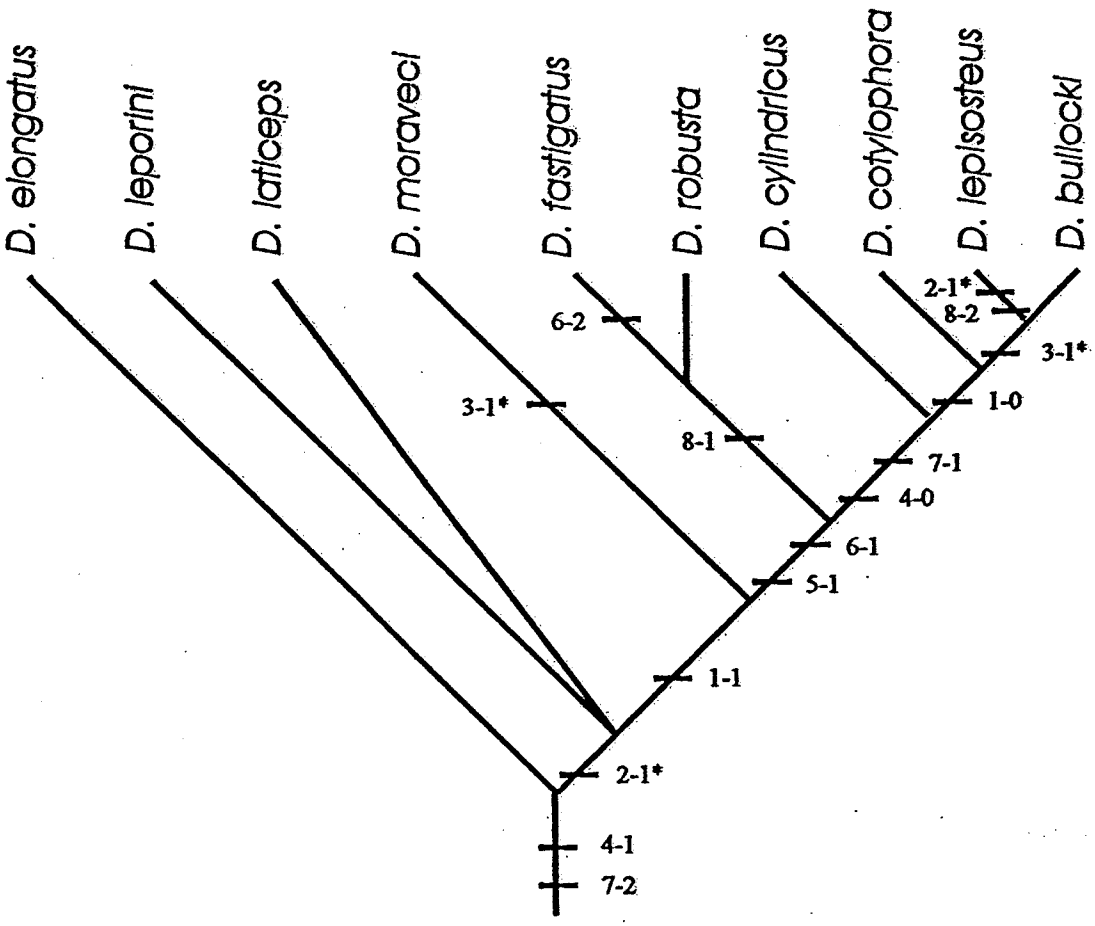
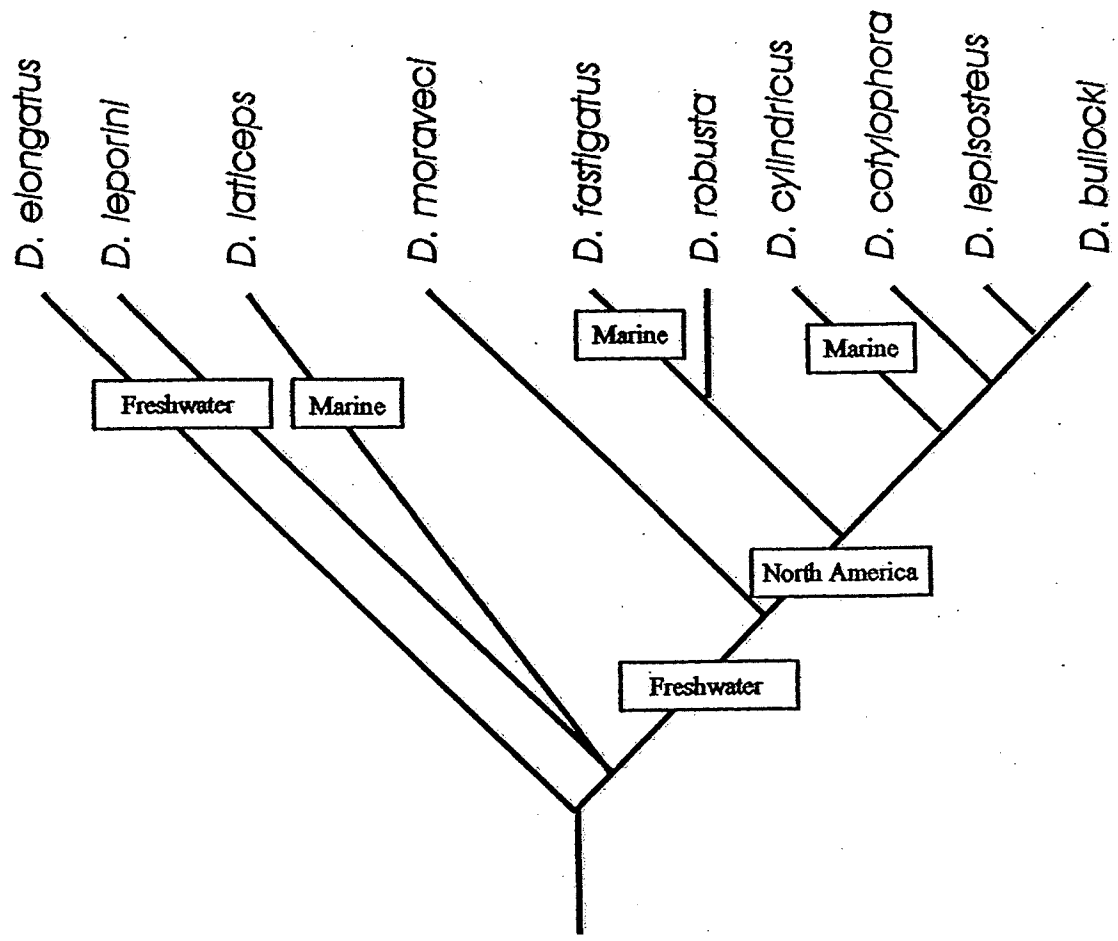

D. elongatus
D. leporini
D. latiiceps
D. moravecl
D. fastigatus
D. robusta
D. cylindricus
D. cotylophora
D. lepisosteus
D. bullocki
2-1*
8-2
3-1*
1-0
7-1
4-0
6-1
5-1
1-1
2-1*
4-1
7-2
6-2
3-1*
8-1

Figure 21. Most parsimonious phylogenetic tree generated by phylogenetic analysis of the data matrix shown in Table 28 for 11 species in the genus *Dichelyne* . Habitat types for the species are mapped on. Letters refer to the following species: A, *D. elongatus*; B, *D. leporini*; C, *D. laticeps*; D, *D. moraveci*; E, *D. fastigatus*; F, *D. robusta*; G, *D. cylindricus*; H, *D. cotylophora*; I, *D. lepisosteus*; J, *D. bullocki*.


D. elongatus
D. leporinl
D. latiiceps
D. moraveci
D. fastigatus
D. robusta
D. cylindricus
D. cotylophora
D. lepisosteus
D. bullocki
Freshwater
Marine
Marine
Marine
North America
Freshwater